Production estimates were made for six samples of Feather moss; mean production was 79±4 g m^{-2} (mean±s.e.). Production, of course, varies with location but the above value compares with the 44 to 58 g m^{-2} (in undisturbed forest) recorded by Weetman and Timmer (1967) in Ontario. It also compares with 38 to 106 g m^{-2} recorded by Tamm (1953, Table V) in Sweden, and with estimates by Wielgolaski and Kjelvik (1975) of 70 to 130 g m^{-2} for Feather mosses in Norwegian subalpine birch forest (extrapolated from Tables 32, 36, and 38) and 70 to 150 g m^{-2} in Salix thicket (extrapolated from Tables 42 and 46).

IV. BRYOPHYTE - ENVIRONMENT INTERACTIONS

1. Laboratory Studies of Net Assimilation

a) Introduction

The correlation between water content and growth of _Tomenthypnum nitens_, and published reports of the importance of water in the physiological ecology of bryophytes (see review by Anderson 1974, pp.68-69), prompted investigation of the relationships between net assimilation and water content of the bryophytes in this study. Previous studies of the effect of water content on net assimilation rates of various bryophytes have been made by Fraymouth (1928), Stålfelt (1937a), Ensgraber (1954), Tallis (1959), Hinshiri and Proctor (1971), Lee and Stewart (1971), Kallio and Heinonen (1973), and Peterson and Mayo (1975). In all cases an optimal water content for net assimilation has been observed, with a decrease in net assimilation rate with decreasing water content until, at very low water contents, no gas exchange is detectable.

Other studies have emphasised the responses of net assimilation to light and temperature, for example Hosokawa _et al_. (1964), Rastorfer and Higinbotham (1968), Bazzaz _et al_. (1970), Rastorfer (1970,1972), Kallio and Karenlampi (1973), and Dilks and Proctor (1975). A major problem with interpreting light and temperature response curves, however, is that both seasonal and short-term acclimation, the alteration of responses to optimally utilize the prevailing conditions, have been reported. Significant seasonal changes in light response curves have been reported by Hosokawa _et al_. (1964) and in temperature response by Stålfelt (1937a). Short-term adjustments to changing temperature and light conditions have been reported by Harder (1925, cited in Kallio and Heinonen 1973) and Rastorfer (1970,1972) [see also criticism of Bazzaz _et al_. (1970) by Longton (1974b)]. Other problems include alteration of light response curves by different temperatures (Tallis 1959; Rastorfer 1970,1972) and the possible effect of carbon dioxide concentration on optimal temperatures. In experiments on some vascular plants, for example, a 1.22% CO_2 concentration raised the optimal temperatures for photosynthesis about 10°C above the optima determined at 0.03% CO_2 with the same light intensity (Lundegårdh 1966, p. 131). It was apparent, therefore, that light and temperature responses of _T. nitens_ and the Feather mosses were likely to be complex and difficult to elaborate. It was decided that this was beyond the scope of this study and attention was therefore focused on the water relations of the species and the effect of water on their net assimilation rates.

Measurement of the relationship between net assimilation and water content, however, provides information which is not readily comparable from one species to another, since the same value for water content may reflect considerable differences in water surplus or water stress in different species (cf. Anderson and Bordeau 1955). To evaluate the effect of water stress on net assimilation, it is desirable to have an index of water status which is readily comparable between different species; an appropriate index for this purpose is water potential. The relationship between water content and water potential was evaluated for each of the species used in this study and water potential values were then used in examining the effects of water status on net assimilation and in comparing and contrasting the effects in the various species.

b) Methods

Mats of _Tomenthypnum_ _nitens_ and the Feather mosses, each 30x55 cm, were collected from the study site in late September and mid October 1975. In order to simulate field conditions, the trays containing the Feather mosses were perforated to allow free drainage, while water was allowed to collect in the _T. nitens_ trays. The mosses were maintained in an Environmental Growth Chamber (Model M12, Chagrin Falls, Ohio) under a clear plastic sheet to reduce evaporation. Incandescent and cool white fluorescent lights provided a light intensity at the moss surface averaging 5700±300 lux (mean±s.e.) for 12 hr with an abrupt light-dark change. The light level was increased to 16900±500 lux for a 4 hr period in the middle of the 12 hr photoperiod. Air temperature was 16°C during the light period with a gradual change to 2°C during the dark period. Plants were sprinkled daily with distilled water and irregularly sprayed with Hoagland's solution, with iron supplied as Fe EDTA.

Net assimilation measurements were made in a second EGC Chamber (Model M3). Positions were marked out on the floor of the chamber and, for each position, light levels which would be received by moss in the experimental flasks (described below) were measured for all combinations of chamber lighting. Light was measured by a quantum sensor (μ Einstein m^{-2} sec^{-1}), a photometer (lux), and a radiometer (watts m^{-2}) (Lambda LI-185 Quantum/Radiometer/Photometer, Lambda Instruments Co., Lincoln, Nebraska).

In small, unventilated chambers high light levels can significantly raise the tissue temperature above ambient air temperature. It was necessary, therefore, to measure this temperature elevation as a function of light intensity. A series of measurements with very fine (0.005 inch) copper-constantan thermocouples attached to moss tissue in experimental flasks showed that temperature elevation (T °C) was related to incoming short-wave radiation (L watts m^{-2}) by the equations:

$$T = 0.043\ L - 0.84 \text{ (for dry moss)}$$

$$\text{and } T = 0.024\ L + 0.25 \text{ (for wet moss).}$$

There is a significant temperature elevation at maximum chamber light levels, i.e. about 17°C for dry moss.

Temperature elevations are lower for wet moss due to energy dissipation through evaporation as well as some reduction of radiation levels by water condensation on the walls of the flask. In experiments where moss temperature was to be kept constant, temperature elevation was compensated for by lowering the chamber temperature by the appropriate amount.

The method used to measure net assimilation was a modification of that described by Larson and Kershaw (1975). A UNOR 2 (H. Maihak, Hamburg, W. Germany) infrared gas analyzer (IRGA), with a carrier reference gas (296 ppm by volume CO_2/air) flowing at 150 ml/min was used to measure the levels of CO_2 within the experimental flasks. The flasks were 500 ml filtering flasks (with a total volume of 580 ml) fitted with rubber stoppers at the top and serum stoppers on the side arms.

The gas-analysis system was similar to that shown in Figure 1c of Larson and Kershaw (1975) except that no drierite column was used. A drying column was considered unnecessary because the IRGA used is relatively insensitive to water vapour (J.M. Mayo, pers. comm. 1976). The IRGA was set at maximum sensitivity, which enabled a precise measure of the immediate change of CO_2 concentration in the sample cell on injection into the carrier stream of a 2.3 ml sample from a gas syringe (Pressure-Lok Series A, Precision Sampling Corp., Baton Rouge, Louisiana).

Larson and Kershaw (1975) state that:

> "Since the CO_2 concentration in the IRGA sample cell, after injection of a 2-ml sample, changes to

> a maximum extent and then rapidly returns to the same concentration as the reference cell, the recorder deflections appear as sharp peaks with a zero line set at the (known) concentration of the reference carrier gas. Peak height is calibrated against known CO_2 concentration by 2-ml injections of the standards. The calibration is accurate to about 5 ppm and linear as long as a constant carrier flow is used."

The linear nature of the calibration, at a constant flow rate, was confirmed in this study.

The experimental procedure for each measurement was as follows: The material to be measured was placed in a flask and the flask stoppered. A 2.3 ml sample of room air was injected into the flask through the serum stopper, the flask agitated to mix the air inside, and a 2.3 ml sample then withdrawn. This procedure was followed in order to maintain the flask gas pressure equal to room pressure. The sample was injected into the IRGA gas stream and the response peak labelled appropriately. This sample represented the CO_2 concentration at the beginning of the experiment. The flask was then placed on its side in one of the marked positions in the growth chamber, where the light had been measured, and left for a certain time period. The time period and amount of moss material were chosen so that the change in CO_2 concentration would be in the region of 40 ppm. This value was considered large enough to minimize the relative magnitude of the measurement errors and small enough to have a minimal effect on moss physiological processes. At the end of the measurement period the flask was removed from the growth chamber, agitated to mix the air, and a 2.3 ml sample withdrawn. This sample was injected into the IRGA stream and the CO_2 concentration at the end of the measurement period determined. The net assimilation (N.A.) rate was calculated as follows:

$$\text{N.A. } (\text{mg } CO_2 \bullet \text{g dry wt}^{-1} \bullet \text{hr}^{-1}) = \Delta CO_2 \text{ (ppm) x } 9.77 \text{ x } 10^{-4} / [\text{dry wt (g) x time (hr)}]$$

The conversion factor of 9.77×10^{-4} was calculated as follows: A 1 ppm change in CO_2 concentration represents 1×10^{-6} mole CO_2/mole air. Since the flask volume is 580 ml, the pressure and temperature in the laboratory averaged 700 mm Hg and 293°K respectively, and 1 mole of gas occupies 22.414 litre at standard temperature and pressure:

$$\text{the conversion factor} = 1 \text{ x } 10^{-6} \text{ x } 580/22414 \text{ x } 700/760 \text{ x } 273/293$$

$$\text{Since 1 mole } CO_2 = 44000 \text{ mg}$$

$$= 1 \text{ x } 10^{-6} \text{ x } (580/22414) \text{ x } 44000$$

$$\text{the conversion factor} = 9.77 \text{ x } 10^{-4} \text{ mg/ppm}$$

The relationship between water potential and water content was evaluated for each of the species by determining water contents of moss samples whose weights had equilibrated over various saturated salt solutions. Saturated salt solutions in closed containers are known to provide precise relative humidities at certain temperatures and these relative humidities can be transformed into water potential values using the equation:

$$\text{water potential (bar)} = (RT/V_w) \ln (RH/100)$$

where R = gas constant (83.14 bar cm^3 $mole^{-1}$ $°K^{-1}$)
T = temperature (°K)
Vw = partial molal volume of water (18.02 cm^3 $mole^{-1}$)

RH = relative humidity (%)

Relative humidity values between 0 and 100% were chosen and salt solutions which provided these humidities were selected from the tables in Winston and Bates (1960). The salts used, their relative humidities and corresponding water potentials are shown in Table 5.

Moss samples were suspended over the saturated salt solutions in small bottles and the bottles were then placed in a water bath maintained at 20±0.3°C. The samples were weighed to equilibrium and water contents then determined from the equilibrium weight and dry weight (80°C). In an attempt to determine if there was a hysteresis effect, i.e. differences in water content at a certain water potential depending on whether the material was wetting or drying, measurements were made on both wetting and drying material.

c) Results

Other workers have noted that physiological responses of various species of moss vary with depth in the canopy (Fraymouth 1928, Abel 1956, Tallis 1959, Willis 1964, Clarke _et_ _al_. 1971, Hinshiri and Proctor 1971, Kallio and Karenlampi 1973). Therefore, to determine which part of the moss was photosynthetically active, a series of measurements of net assimilation rates of material from various depths in the canopy was made for each of the four species. The means and standard errors are presented in Table 6. There is a

Table 5. Relative humidities and corresponding water potentials over saturated salt solutions at 20°C. Relative humidity values from Winston and Bates (1960).

Compound	Relative Humidity (%)	Water Potential (bar)
distilled water	100.0	0
potassium sulphate	98.0	-27
lead nitrate	97.0	-41
potassium phosphate, monobasic	96.5	-48
pyrocatechol	95.5	-62
potassium nitrate	93.5	-91
magnesium sulphate	90.0	-143
potassium chloride	85.0	-220
ammonium sulphate	80.5	-293
sodium chloride + potassium chloride	70.0	-482
calcium nitrate	55.5	-796
magnesium chloride	33.0	-1500
potassium acetate	20.0	-2177
lithium chloride	12.5	-2813

considerable decrease in capacity for net photosynthesis with depth, so care was taken to ensure that comparable material was used for all subsequent experiments.

Anderson (1974) noted that "there is a complicated

Table 6. Net assimilation rates at various depths in the moss canopies (mg $CO_2 \bullet$ g dry $wt^{-1} \bullet hr^{-1}$). Light level 250 μ Einstein m^{-2} sec^{-1}, temperature 15°C. Values are means with standard errors in parentheses. Values for _Hylocomium splendens_ are for successive annual layers down from the canopy surface.

Species	Depth in Canopy (cm)			
	0-1.5	1.5-3.0	3.0-4.5	4.5-6.0
Hylocomium splendens	3.38 (±0.256)	1.99 (±0.082)	0.27 (±0.072)	-0.21 (±0.037)
Pleurozium schreberi	3.02 (±0.246)	0.89 (±0.128)	-0.36 (±0.023)	-0.41 (±0.046)
Ptilium crista-castrensis	2.91 (±0.171)	1.12 (±0.092)	-0.05 (±0.052)	-0.37 (±0.092)
Tomenthypnum nitens	1.20 (±0.033)	0.16 (±0.033)	-0.04 (±0.022)	-0.14 (±0.013)

interaction among photosynthetic rates, light intensity, and water content of the moss." Temperature is foremost among other complicating factors which should be added to this list. In the investigation of the effects of water content on photosynthetic rates it was considered desirable to hold the light level and temperature at or near an optimal level in order to avoid potential complications due to limiting effects of these parameters.

To determine optimal light levels, measurements of net assimilation of _Hylocomium splendens_ and _Tomenthypnum nitens_ were made at various light intensities. The results are shown in Figs. 19 and 20 respectively. Light response curves of Pleurozium schreberi and Ptilium crista-castrensis were not measured, but were assumed to be similar to that of H. splendens. The abscissa in Figs. 19 and 20 shows "photosynthetically active radiation" (PAR), i.e. quanta in the 400-700 nm range, plotted on a logarithmic scale.

These Figures show that the light compensation points are about 4 and 7 µ Einstein m^{-2} sec^{-1} respectively for H. splendens and T. nitens. Measurements indicated that these values corresponded to about 300-500 lux, which is similar to the 300-700 lux reported by Stålfelt (1937a) for forest mosses and the observation by Kallio and Karenlampi (1973) that the light compensation of mosses at optimum temperatures is around 400 lux.

Maximum photosynthetic rates for Hylocomium splendens were recorded at about 250 µ Einstein m^{-2} sec^{-1}, which corresponds to about 14000 lux. This value is similar to the 16000 lux reported for H. splendens at 15°C by Stålfelt (1937a). Light levels in excess of this value resulted in a lower net assimilation rate, a phenomenon which has been frequently observed in mosses which grow in shaded habitats (for example Stålfelt 1937a; Tallis 1959, 1964; Hosokawa et al. 1964; Willis 1964; Rastorfer and Higinbotham 1968; Rastorfer 1970; and Kallio and Heinonen 1973). This depression of net assimilation has been attributed to the damaging effect of high levels of visible radiation, rather than UV, on the photosystems of the plants (Levitt 1972,

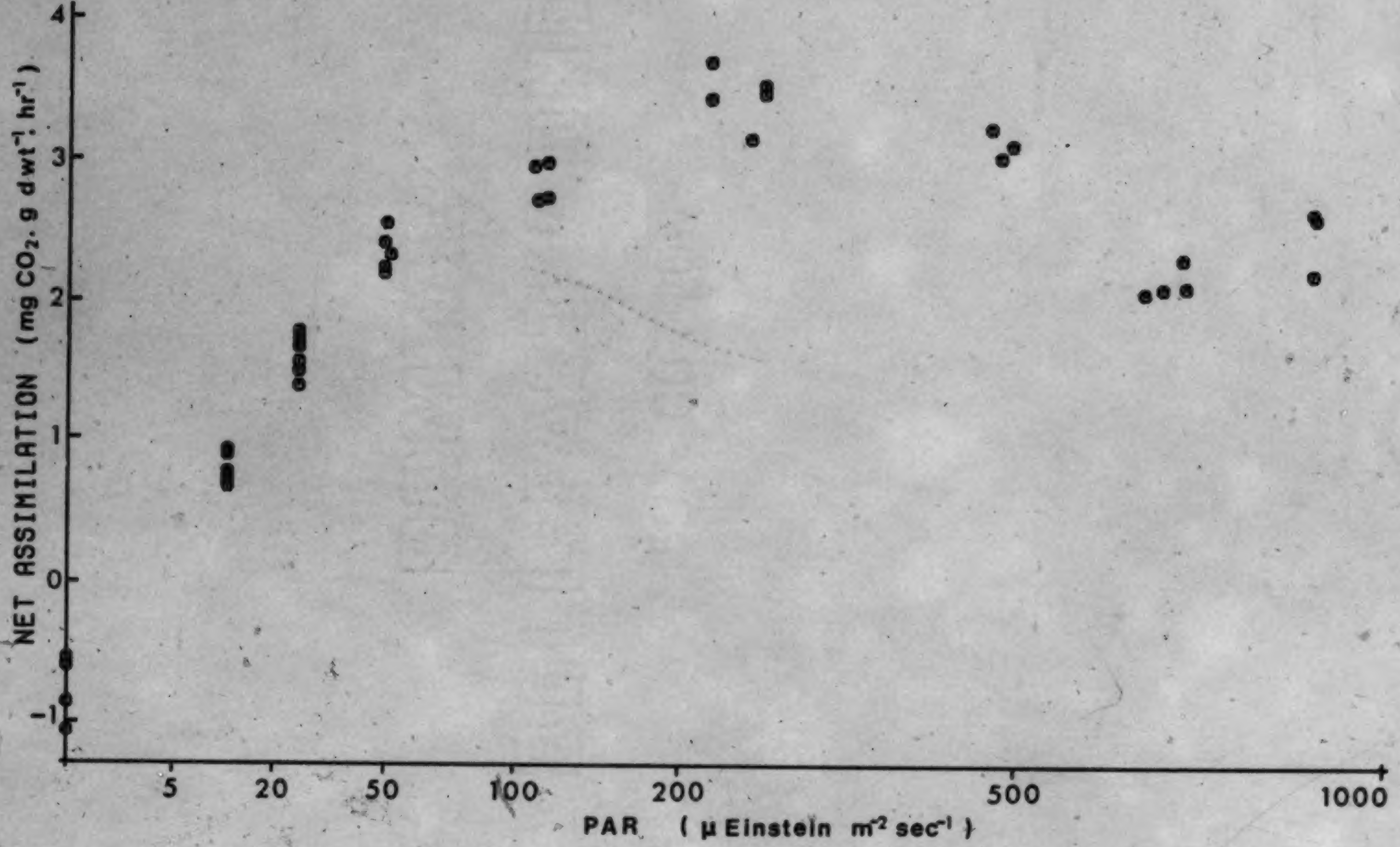

Figure 19. Light response curve of Hylocomium splendens at 15^{o}C. PAR = Photosynthetically Active Radiation (400 - 700 nm).

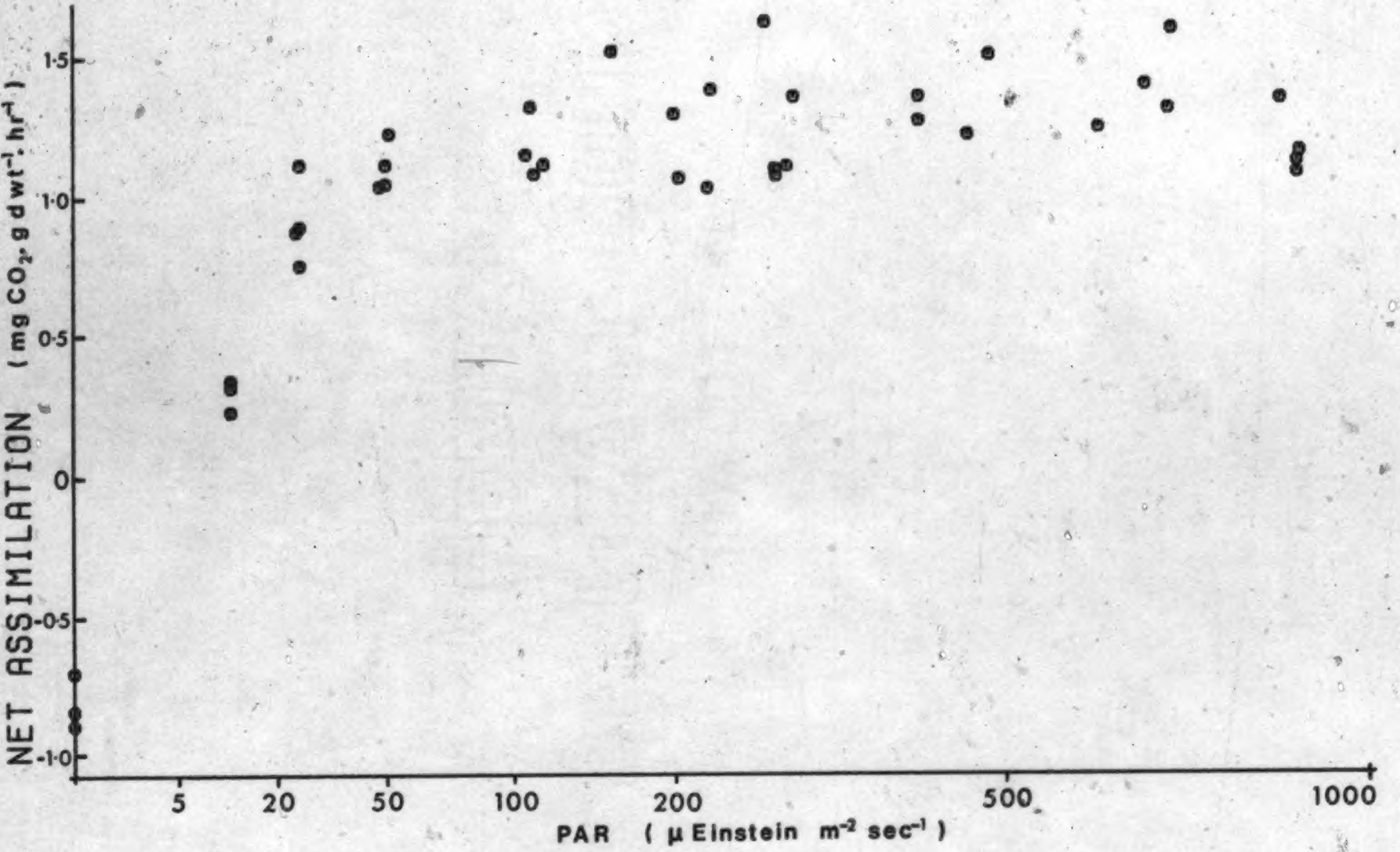

Figure 20. Light response curve of Tomenthypnum nitens at 15^{o}C.
PAR = Photosynthetically Active Radiation (400 - 700 nm).

p.451).

Maximum photosynthetic rates for Tomenthypnum nitens were recorded at about 150 µ Einstein m^{-2} sec^{-1}, which corresponds to about 8000 lux. There were no apparent deleterious effects at high light levels, at least during the measurement periods used (30-35 min). The "light saturation" values of these bryophytes are comparable with the 10000 to 20000 lux range reported for many bryophyte species (Hosokawa et al. 1964, Kallio and Karenlampi 1973).

A light level of 250 µ Einstein m^{-2} sec^{-1}, being close to optimal for the species under laboratory conditions, was therefore considered appropriate for subsequent experiments. Whether the results in the laboratory are applicable to the field remains to be established. The optimal light level for H. splendens (14000 lux) is close to the maximum light level in the storage growth chamber (17000 lux), which may reflect normal physiology or result from acclimation. This value is also higher than that measured for T. nitens but whether this has any significance is not known. "Light saturation" for T. nitens occurred at approximately 0.1 cal cm^{-2} min^{-1}, which is less than 10% of the maximum intensities in its normal habitat. Net assimilation rates, however, remained fairly constant at light intensities up to 0.59 cal cm^{-2} min^{-1} (about one-half full sunlight), so it is possible that this species is adapted to a wide range of light intensities, and retains this adaptation, at least for periods up to 2.5 months, when grown under the same conditions as the Feather mosses.

Because of time and equipment constraints, no attempt was made to measure temperature response and determine optimal temperatures for the species studied. Stålfelt (1937a) found that optimal temperatures for forest mosses in Sweden were typically in the range 15-20°C, with Hylocomium splendens having an optimal temperature of 18°C. Kallio and Heinonen (1973) measured the temperature responses of Pleurozium schreberi from southern Finland and reported an optimal temperature of 15°C. There are no known reports of optimal temperatures for Tomenthypnum nitens. Since the 'day' temperature in the growth chamber was 16°C and the mosses were presumably acclimated to these conditions, it was assumed that an experimental temperature of 15°C would not be limiting, an assumption which, though plausible, remains to be confirmed.

Measurements of the influence of water content on net assimilation rate, therefore, were made at a light level of 250 µ Einstein m^{-2} sec^{-1} and a moss temperature of 15°C. The results for the four species are presented in Figs. 21 to 24. All the Figures show a broadly similar relationship between water content and net assimilation rate. In each case gas exchange ceases when the water content falls below 0.4 g • g dry wt^{-1} and in at least three of the species there is an indication that desiccation affects photosynthesis more severely than it does respiration, confirming observations by Mayer and Plantefol (1926) and

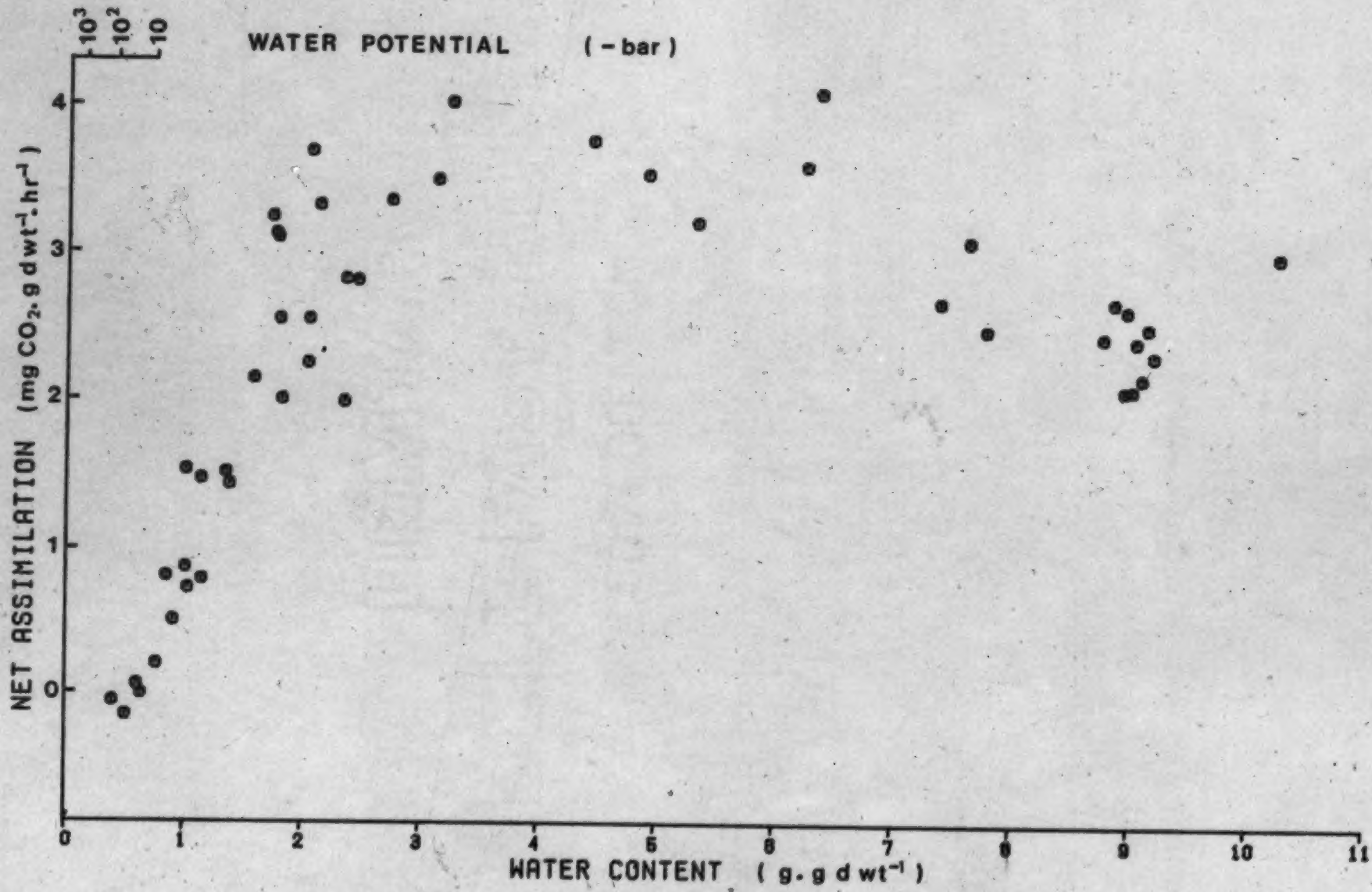

Figure 21. Effect of water status on net assimilation of Hylocomium splendens at 15°C and 250 µ Einstein m^{-2} sec^{-1}.

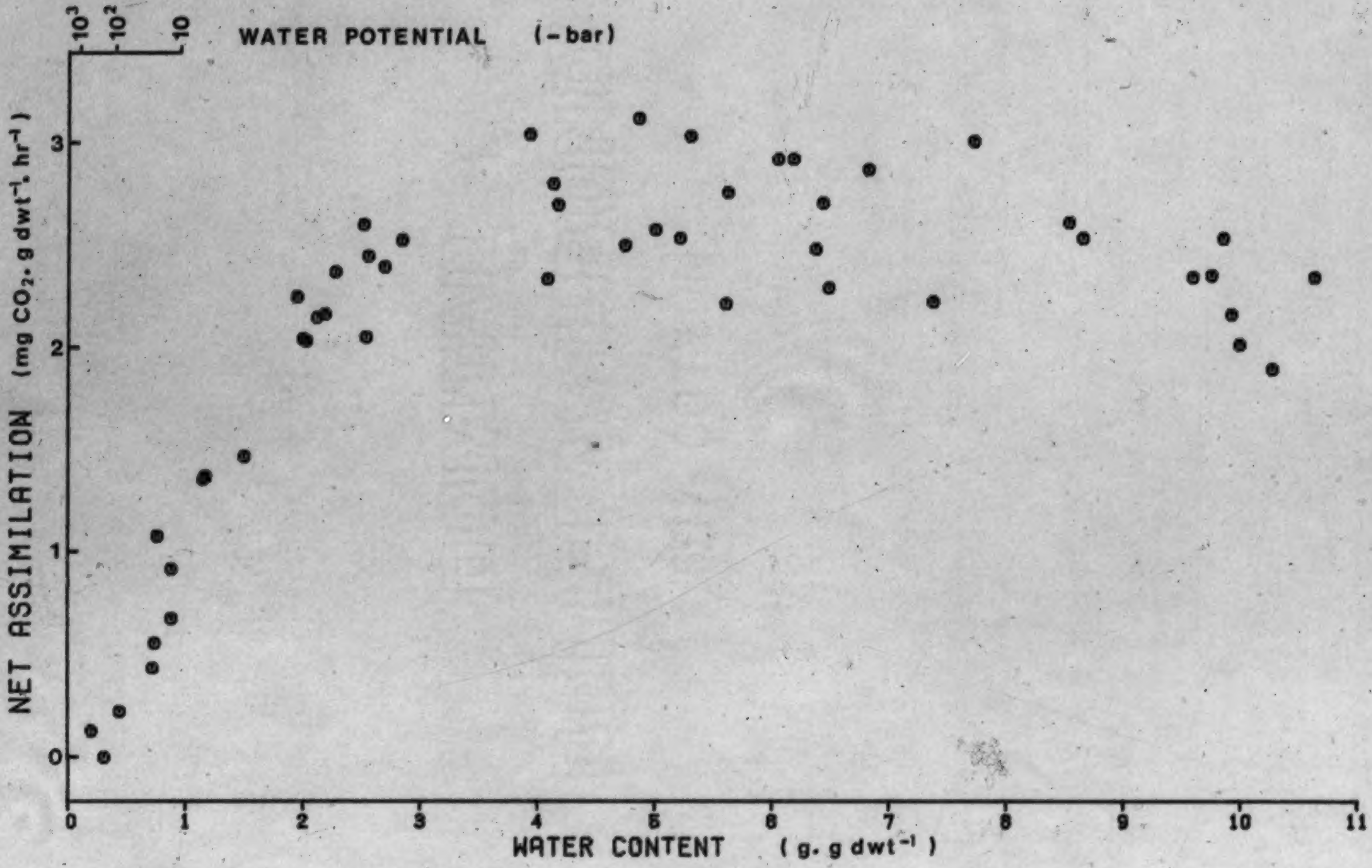

Figure 22. Effect of water status on net assimilation of *Pleurozium schreberi* at 15°C and 250 μ Einstein m^{-2} sec^{-1}.

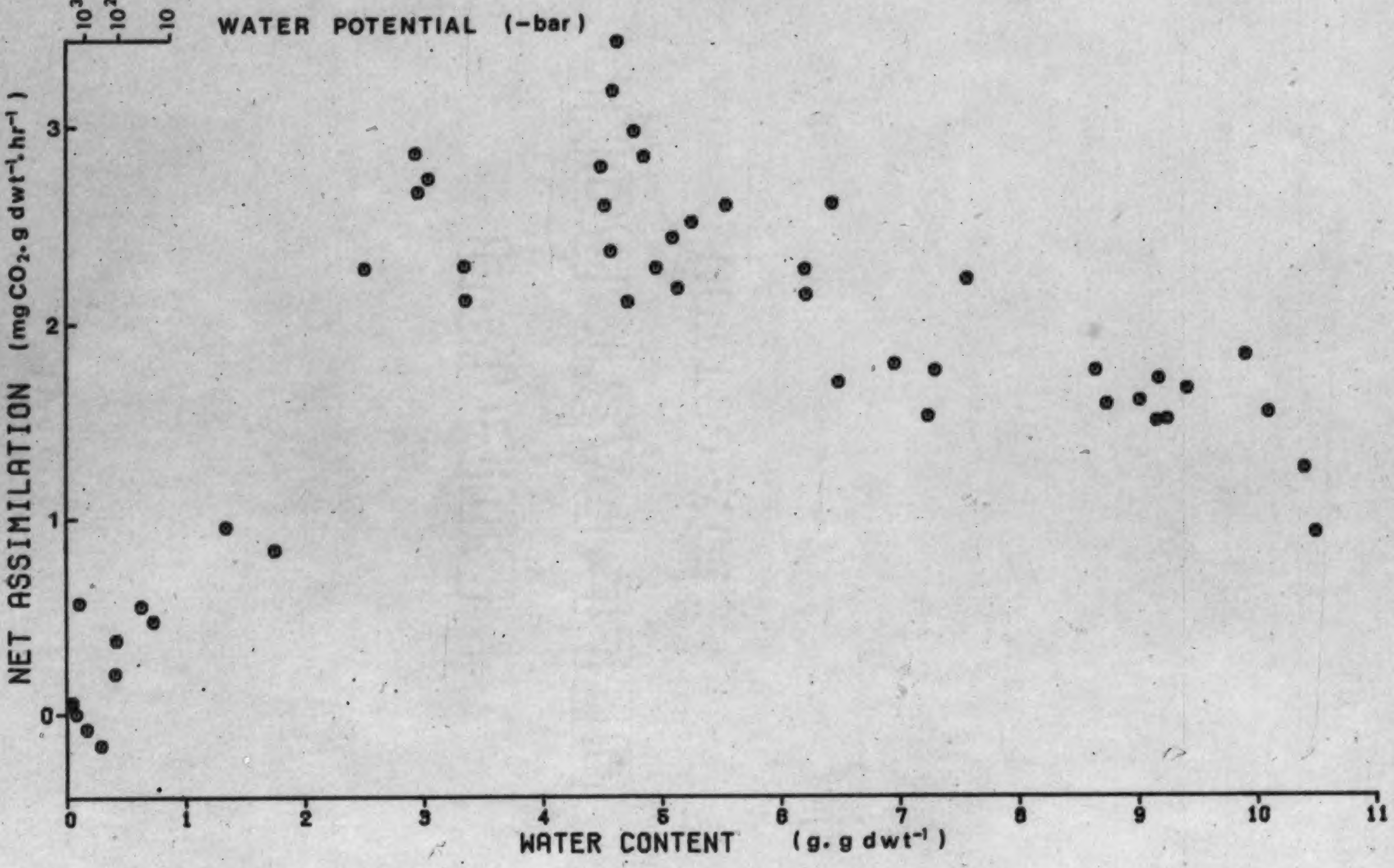

Figure 23. Effect of water status on net assimilation of Ptilium crista-castrensis at 15°C and 250 µ Einstein m^{-2} sec^{-1}.

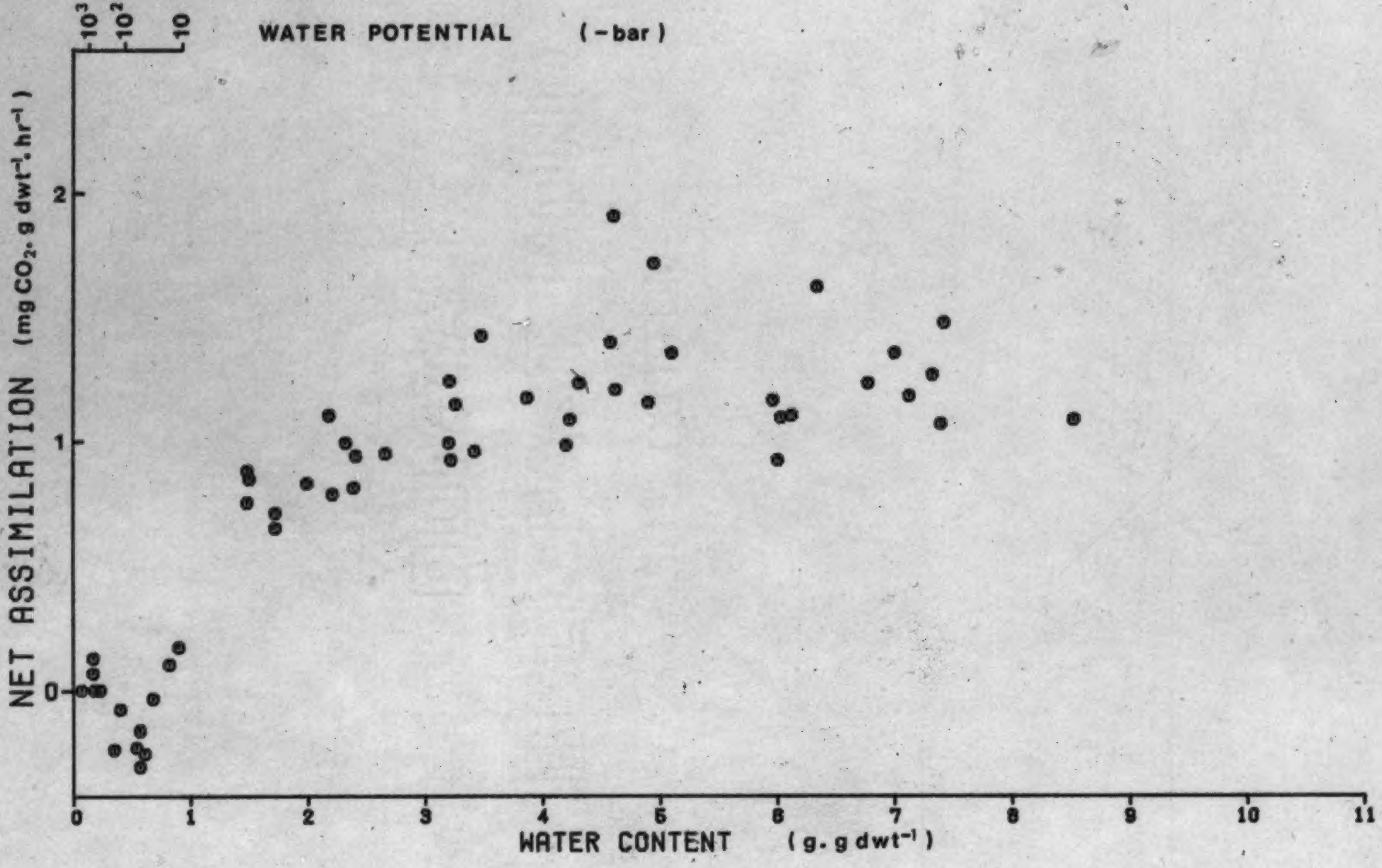

Figure 24. Effect of water status on net assimilation of Tomenthypnum nitens at 15°C and 250 μ Einstein m^{-2} sec^{-1}.

Plantefol (1927) (both cited in Patterson 1964) (see also Slatyer 1967, p.292). This differential effect is most obvious in *Tomenthypnum nitens* (Fig. 24), the species which grows in the wettest habitats, and was not detected in *Pleurozium schreberi* (Fig. 22), the species considered to grow in the driest habitats (e.g. Abel 1956). This phenomenon is unlikely to have a direct effect on relative growth rates but may reflect important differences in cell physiology, particularly with regard to drought tolerance.

There is also a distinct depression of net assimilation rates at high water contents, a phenomenon which has been observed in many bryophyte species and generally attributed to the resistance to gas exchange of water films on the moss surface (Fraymouth 1928, Stålfelt 1937a, Tallis 1959).

The optimal water content for net assimilation in *Hylocomium splendens* was found to be between 3 and 6 g • g dry wt^{-1} (Fig. 22), which is comparable with 2 to 4 g • g dry wt^{-1} reported by Stålfelt (1937a). The optimal water content for *Pleurozium schreberi* was also between 3 and 6 g • g dry wt^{-1} (Fig. 23), and comparable with 2 to 4 g • g dry wt^{-1} reported by Kallio and Heinonen (1973). The differences between the experimental and published values may be due to differences in gametophyte morphology in different populations, physiological adaptation, or differences in technique.

The average net assimilation rate recorded for *Hylocomium splendens* at optimal water contents was 3.7 mg

CO_2 • g dry wt^{-1} • hr^{-1} (all subsequent values are in these units). This is close to the 3.2 reported by Stålfelt (1937a) and 2.5 reported by Kallio and Karenlampi (1973). The average rate for Pleurozium schreberi was 2.9, compared with 2.0 reported by Stålfelt (1937a) and 1.1 by Kallio and Karenlampi (1973). The value for Ptilium crista-castrensis was 2.8, compared with 3.4 reported by Stålfelt (1937a). The average rate for Tomenthypnum nitens was 1.3, and no previously published values are known.

Relationships between water content and water potential for Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis, and Tomenthypnum nitens are presented in Figs. 25 to 28. It can be seen that there are no significant differences between wetting and drying curves and that differences among the species are minor. In fact the relationships for the species in this study are similar to those obtained by Klepper (1963) for Dicranum scoparium, Willis (1964) for Tortula ruraliformis, and by Bayfield (1973) for Rhacomitrium lanuginosum (when re-calculated and plotted to the same scale). The small differences between the species could well reflect differences in cell wall structure, cell matric and osmotic potentials, or other parameters which could be important in tolerance of and recovery from desiccation, but this has yet to be established.

Water potential values of -10, -100, and -1000 bar are indicated on Figs. 21 to 24. Values closer to zero are

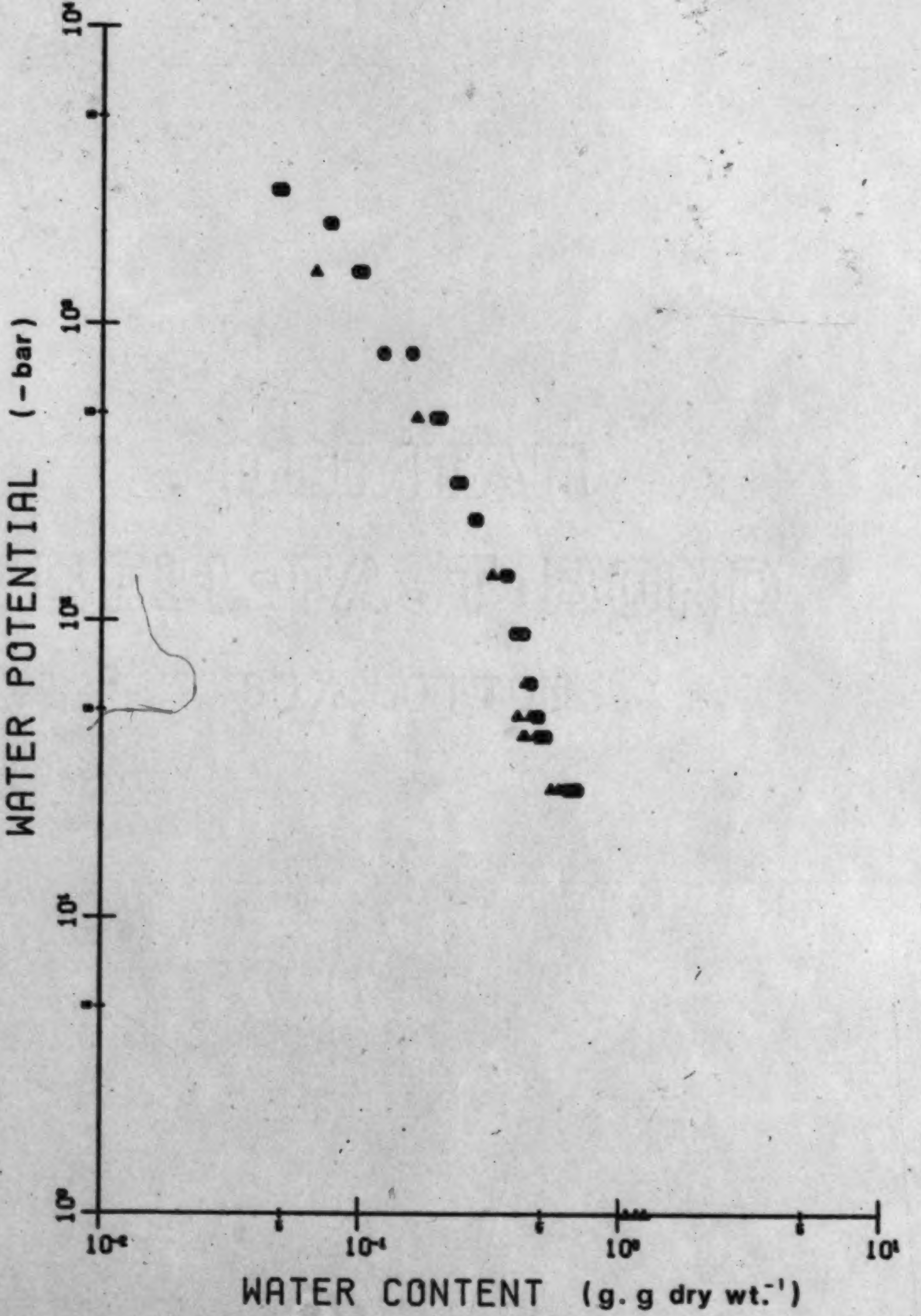

Figure 25. *Hylocomium splendens*: water potential vs. water content. ○ = drying curve; ▲ = wetting curve.

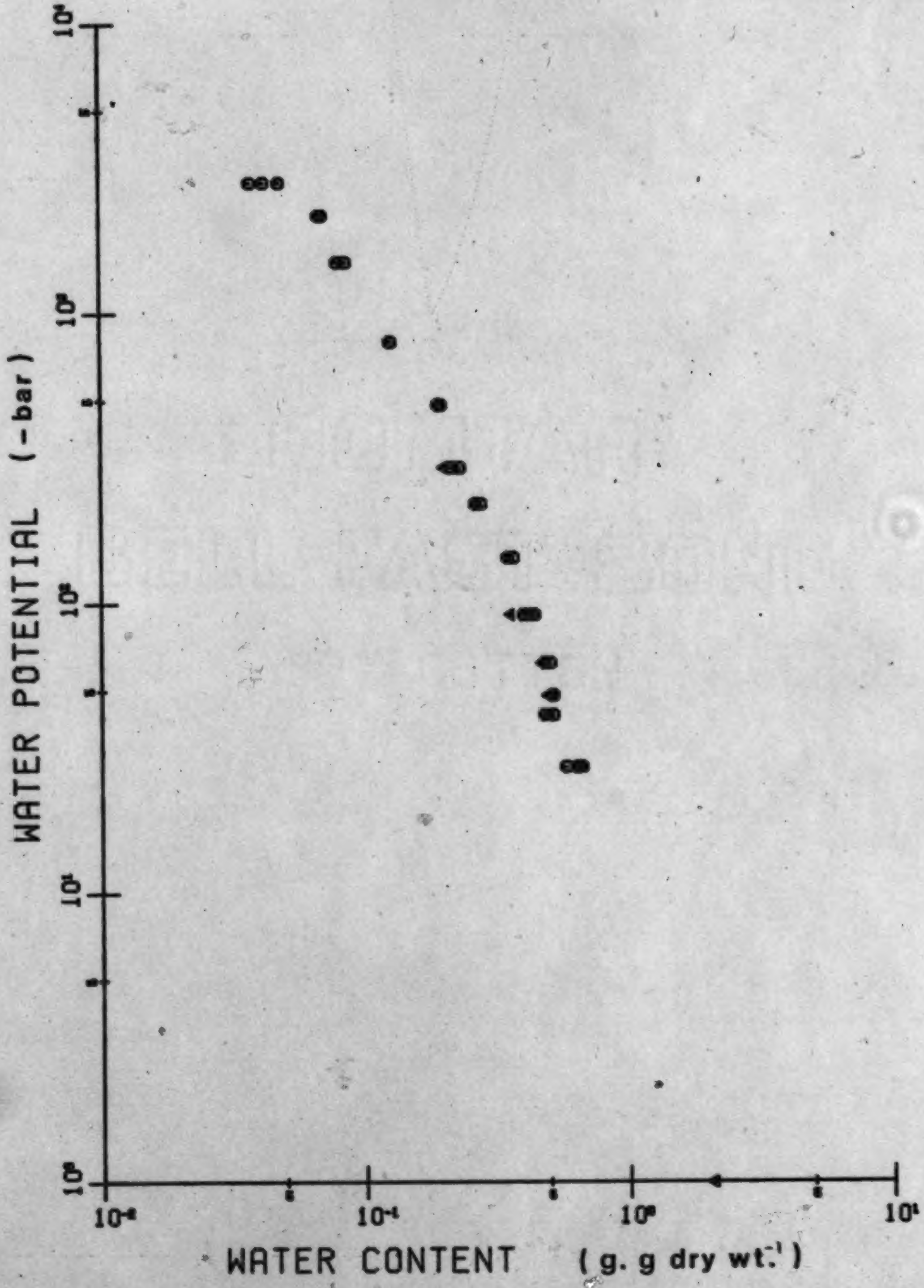

Figure 26. *Pleurozium schreberi*: water potential vs. water content. O = drying curve; ◄ = wetting curve.

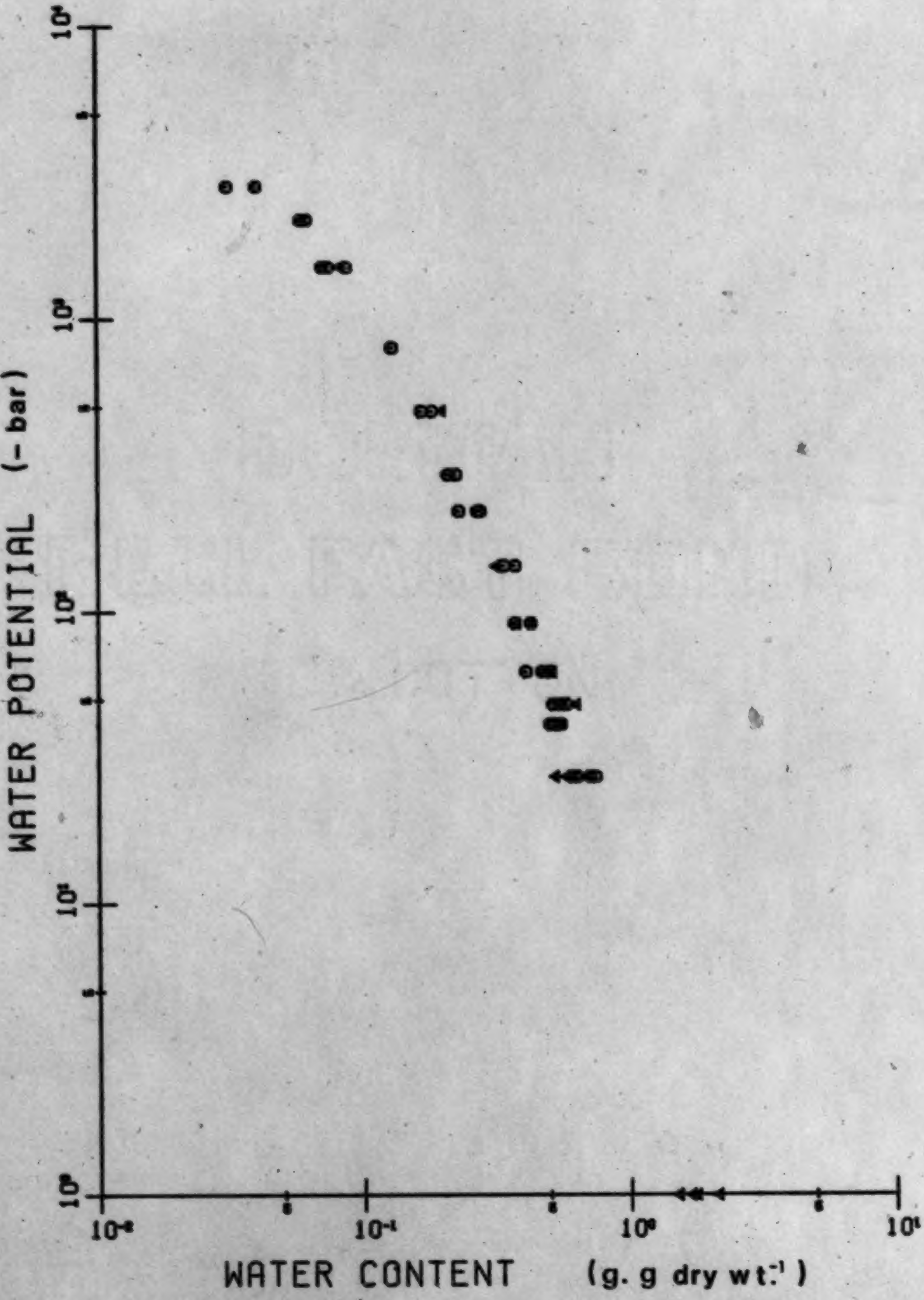

Figure 27. Ptilium crista-castrensis: water potential vs. water content. ○ = drying curve; ◄ = wetting curve.

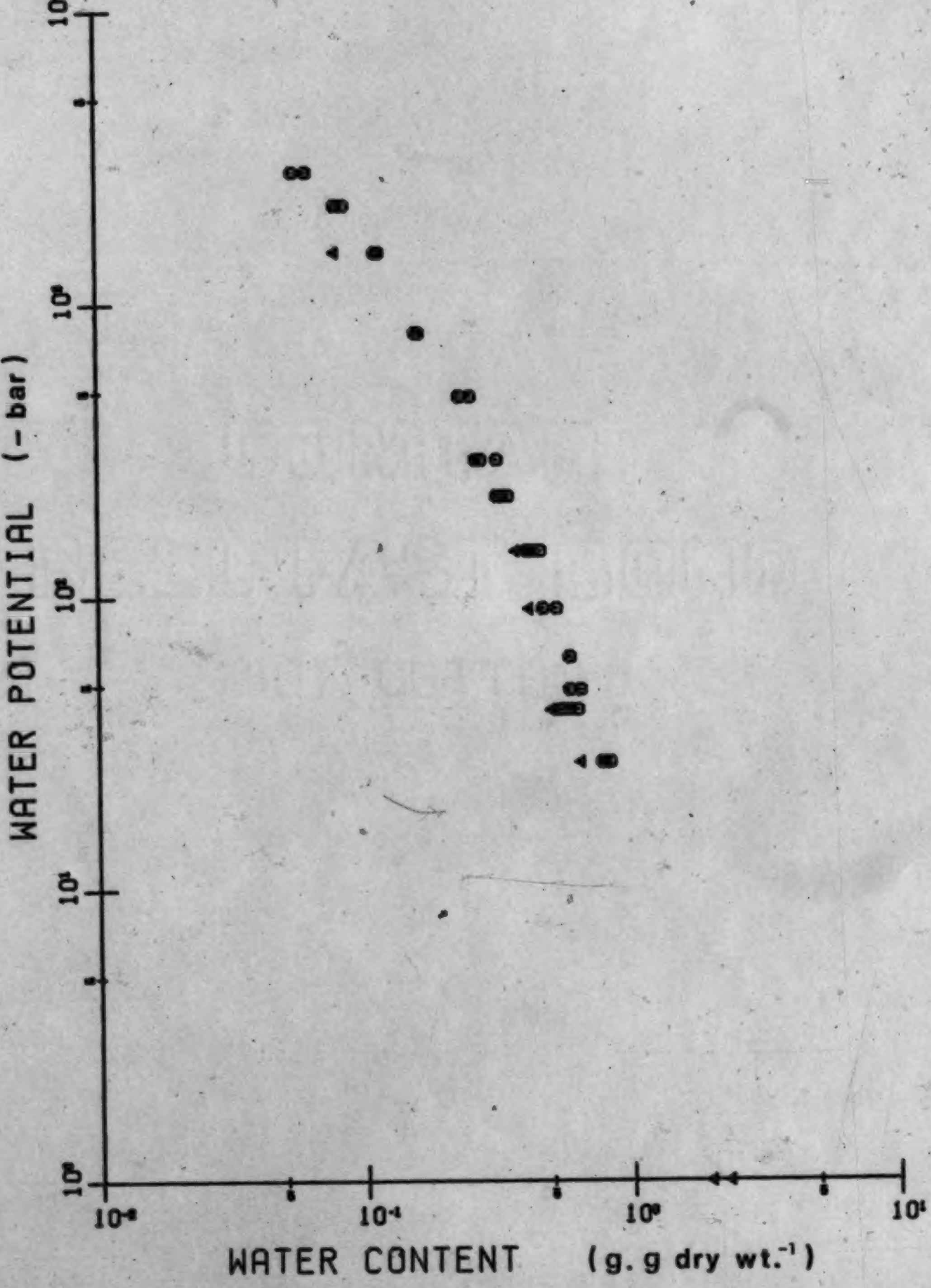

Figure 28. *Tomenthypnum nitens*: water potential vs. water content. ○ = drying curve; ◄ = wetting curve.

difficult to determine. The water contents of mosses near equilibrium over distilled water are all in the region of 1.5 to 2.5 g • g dry wt^{-1}, so water potentials must be close to zero at these values. They will be slightly less than zero, however, because of osmotic and matric potentials, particularly in the cell walls (cf. Slatyer 1967, p.148).

There is a significant decline in net assimilation rates in all species at water potentials between 0 and -10 bar. This is in agreement with Slatyer's (1967, p.292) statement that "In general, reductions in apparent photosynthesis occur at water potentials close to zero." The effect of water stress on net assimilation rates appears to be similar in all four species.

Water contents at equilibrium over distilled water are much lower than the water contents of saturated moss. Maximum water contents for the four species were determined by saturating the mosses with water and allowing them to drain for several minutes before sampling. The following water contents (g • g dry wt^{-1}) were obtained: _Hylocomium splendens_ 12.5, _Pleurozium schreberi_ 15.7, _Ptilium crista-castrensis_ 17.1, and _Tomenthypnum nitens_ 10.9. Since the equilibrium water contents of the mosses over distilled water were only 10-20% of these values, the data suggest that some 80-90% of the water retained by saturated moss is held externally in leaf axils and in capillary films on the leaves and stems. Presumably the water contents over distilled water mark the boundary between "internal" and "external" water, concepts which have been used frequently in studies of bryophyte ecology (e.g. Gimingham and Smith 1971, Hebrard 1974). No water stress occurs until this "external" water has evaporated, and the time taken for this to happen is the time during which photosynthesis can take place.

One complicating factor, however, is that photosynthesis rarely commences immediately upon wetting. There is generally a delay, the length of which depends on several factors, some of which have been previously investigated, for example by McKay (1935), Stålfelt (1937a), Patterson (1943), Tallis (1959,1964), Hinshiri and Proctor (1971), Lee and Stewart (1971), Bewley and Thorpe (1974) and Peterson and Mayo (1975). It appears that the duration of the delay depends, among other factors, on the species, the duration of the previous dry period, and the number of prior wetting/drying cycles.

An additional feature of interest is the pronounced respiration burst detectable immediately after wetting (see also Willis 1964, Hinshiri and Proctor 1971, Proctor 1972, Bewley and Thorpe 1974, Bewley _et al_. 1974, Dilks and Proctor 1974, Bewley and Gwóźdź 1975, Peterson and Mayo 1975). Respiration rates for the Feather mosses in the first 10 min after wetting are presented in Table 7. These respiration rates, which were measured at 250 µ Einstein m^{-2} sec^{-1} and 15°C, are considerably higher than the dark respiration rates of metabolically "normal" moss at 15°C,

Table 7. Respiration 0-10 min after wetting (at 250 μ Einstein m^{-2} sec^{-1} and 15°C) compared with respiration in the dark at 4°C and 15°C (mg CC_2 • g dry wt^{-1} • hr^{-1}). Values are means with standard errors in parentheses.

Species	0-10 min After Wetting	Respiration in the Dark	
		15°C	4°C
Hylocomium splendens	-1.46 (±0.029)	-0.73 (±0.099)	-0.31 (±0.034)
Pleurozium schreberi	-2.18 (±0.113)	-0.81 (±0.033)	-0.34 (±0.020)
Ptilium crista-castrensis	-2.53 (±0.137)	-0.77 (±0.044)	-0.34 (±0.022)
Tomenthypnum nitens	---	-0.82 (±0.057)	-0.40 (±0.005)

normal in this case meaning moss which is capable of carrying out photosynthesis in the light. Dark respiration rates increase with temperature (compare the rates at 15°C with those at 4°C in Table 7), but the rates achieved in the first 10 min after wetting are considerably higher than dark respiration rates at temperatures likely to occur in the field. This indicates that metabolic pathways different from those involved in normal dark respiration are involved, a problem which has been investigated by Bewley and Thorpe (1974) and Bewley and Gwóźdź (1975) among others.

2. External Anatomy and Water Movement

The complex relationships between water potential and "internal" and "external" water, and effects of water on the initiation, maintenance, and decline of net assimilation, prompted an investigation of the source, distribution, and loss of water in the moss canopy systems.

The primary source of water in the mire complex is rainfall, however ground water in the fen is apparently a significant source for Tomenthypnum nitens. Measurements of apical water contents in this species in early July 1975 showed water contents of up to 4.6 g • g dry wt^{-1} three days after rain, and over 3 g • g dry wt^{-1} ten days after rain. Since evaporation stress during this period was very high (Fig. 12, p.53), the most likely explanation for these high water contents is supply of water from below.

The Feather moss species, on the other hand, occupy better drained sites (Birse 1958a). Tamm (1953, pp.82-101) discussed the supply of nutrients and water to Hylocomium splendens and concluded (p.101) that "The old view that Hylocomium splendens and similar mosses obtain their nutrients and water from below meets with serious difficulties when it comes to the interpretation of the experimental results" (see also Watson 1960). The primary source of water for the Feather mosses, therefore, appears to be precipitation, which raises the question of the extent to which external anatomy and canopy morphology of the different species are adapted to the source and direction of movement of the water supply.

Morphological features which most strongly influence direction and rate of external water movement are density and orientation of the stem leaves (cf. Bowen 1931; Mägdefrau 1935; Anderson and Bordeau 1955; Barkman 1958, p.78; and Tallis 1959) and the presence of a tomentum of rhizoids, or paraphyllia (Richards 1959). Structure and/or chemical composition of the external surface of the leaf and stem also appear to be important in reducing surface tension, thus facilitating movement of water up the stem.

The height to which water can rise by capillarity on the outside of individual gametophytes was investigated by observing the distance which water moved up dry stems cut to certain lengths and placed with their bases in water in small glass cylinders. In all species water was able to reach the apex from a depth of 4 cm and in all except *Pleurozium schreberi* water reached the apex from a depth of 6 cm. In *Hylocomium splendens* and *Tomenthypnum nitens*, water was able to reach the stem apex from a depth of 8 cm, presumably due to the presence of paraphyllia on the stem of the former and the dense tomentum of rhizoids on the leaf bases of the latter.

The increasing resistance to water movement with depth observed in the Feather mosses appears to be due to decomposition and eventual loss of stem leaves. This loss of stem leaves was observed in all the species and is probably responsible for the decrease in capacity for net assimilation with depth which was previously discussed. Near the apical region of the stems, water movement appears to proceed in the following way: liquid water reaches the base of the first leaf, the cells and/or cell walls at the leaf base absorb the water and the leaf begins to expand. Simultaneously water moves rapidly up the folds in the leaf towards the leaf apex and from there moves out across the entire lamina. As the leaf expands away from the stem more water is drawn into the leaf axil, which acts as a reservoir from which water eventually rises into the axil of the next leaf up the stem, and so on.

The species best adapted for external water transport up the stem appears to be *Tomenthypnum nitens* with its dense tomentum, followed by *Hylocomium splendens*, *Ptilium crista-castrensis* and then *Pleurozium schreberi*. Even though there is considerable variation among different populations of the same species in stem morphology and extent of decomposition, there appears to be a close link between water transport adaptations and habitat; *T. nitens* grows in the wettest sites while the habitat of *P. schreberi* is comparatively xeric.

The four species also differed in the extent to which water was able to move from the apex down the stem. Experiments were conducted in which drops of water were added to the apices of dry stems and the subsequent movement of the wetting fronts observed. In *Tomenthypnum nitens* water moved freely through the tomentum to the stem base. Since this species has a comparatively low water holding capacity (see section IV.3.c above), this suggests that much of the rain falling on the moss in the field would be transported down through the canopy and added to the ground water supply, rather than retained in the apical region. Transport of water away from the apical region would prevent inhibition of net assimilation by high water contents (IV.3.c), and the incorporation of this water into the ground water table would allow re-transport of water up the stems on a future occasion when evaporation stress was high. It is possible, however, that a low resistance to water transport down the stem confers no particular advantages to the species but is simply a corollary of low resistance to transport up the stem.

In the Feather mosses water moved via the stem leaves, as in upward transport, but the process was somewhat different. Instead of moving into the leaf axil and then building up until drawn into the axil of a leaf higher up the stem, as described above, the water builds up in the leaf axil but tends not to move to the one below it unless it physically overflows into it. In other words, unless the amount of water available to move down the stem is high, the water tends to remain in the region of the apex. It will be shown in a later section how the tendency of water to remain in the region of the apex after rain might be advantageous to the Feather mosses while possibly having an inhibitory effect on _T. nitens_.

Resistance to water movement in either direction would probably increase as water content decreased and the capillary connections between the leaves and along the stem were broken. Vertical water movement would be expected to decrease significantly at this point, even though a considerable gradient in water potential may develop. Peterson and Mayo (1975), for example, reported a water potential gradient of 15 atm over a distance of 4 cm in _Dicranum polysetum_ and supported the suggestion of Anderson and Bordeau (1955) that water is not transported under these conditions but used locally by the adjacent leaves.

3. Microclimate and Bryophyte Growth

a) *Tomenthypnum nitens*

The correlations between length increase and colour of the apical region and between colour and water content raised the question of whether differences in water content were responsible for the differences in growth rates. It was shown above (III.2) that, in nine samples, water contents of moss with green apices averaged 3.44±0.23; with yellow apices 2.09±0.14; and brown, 0.35±0.11 g • g dry wt^{-1} (mean±s.e.). When these water content values are examined with respect to the net assimilation *versus* water content curve in Fig. 24, it is apparent that the water content of material with green apices corresponded to 90% of the maximum net assimilation, and that of yellow apices averaged 67% of the maximum. At a water content corresponding to that of brown apices, there is either no gas exchange or a net loss of carbon. It would appear, therefore, that, assuming that growth is correlated with net assimilation rate, differences in apical water contents were responsible for the differences in growth rate of the various colour categories of *Tomenthypnum nitens* in the field.

Rates of length increase in the various colour categories show some variation during the season (Fig. 16). Assuming that growth is closely related to length increment, it can be seen that growth rates increased from May to June then showed a more or less steady decrease until October. A similar seasonal growth pattern has been reported for _Aulacomnium palustre_ by Teczynska-Kamecka (1974). Growth rates were probably low during early May because the ground water in the fen was frozen (Fig. 10, p.48), and low temperatures in the moss canopy probably also contributed to limiting growth in October.

Since apical water contents appeared to be responsible for differences in growth rates, changes in growth rate during the season might be correlated with changes in one of the parameters affecting the water contents. Mean length increments for each colour in each month were calculated as a percentage of the total length increment for that colour during the season and these are shown in Table 8. Moss with brown apices showed no growth during the season and was not included. Growth of moss of this category after mid-August was due to the production of new shoots which will be discussed below.

The mean percentages from Table 8 were compared with total monthly precipitation (Fig. 29e) and the correlation coefficient was found to be 0.92. This high correlation suggests that rainfall had some direct or indirect effect on growth. Rainfall could affect growth either through the frequency of precipitation or through some form of rain water storage, where the amount of growth after rain is proportional to the amount stored. Frequency of rain was considered to be a minor factor since the correlation between growth and the number of wet days in each month was

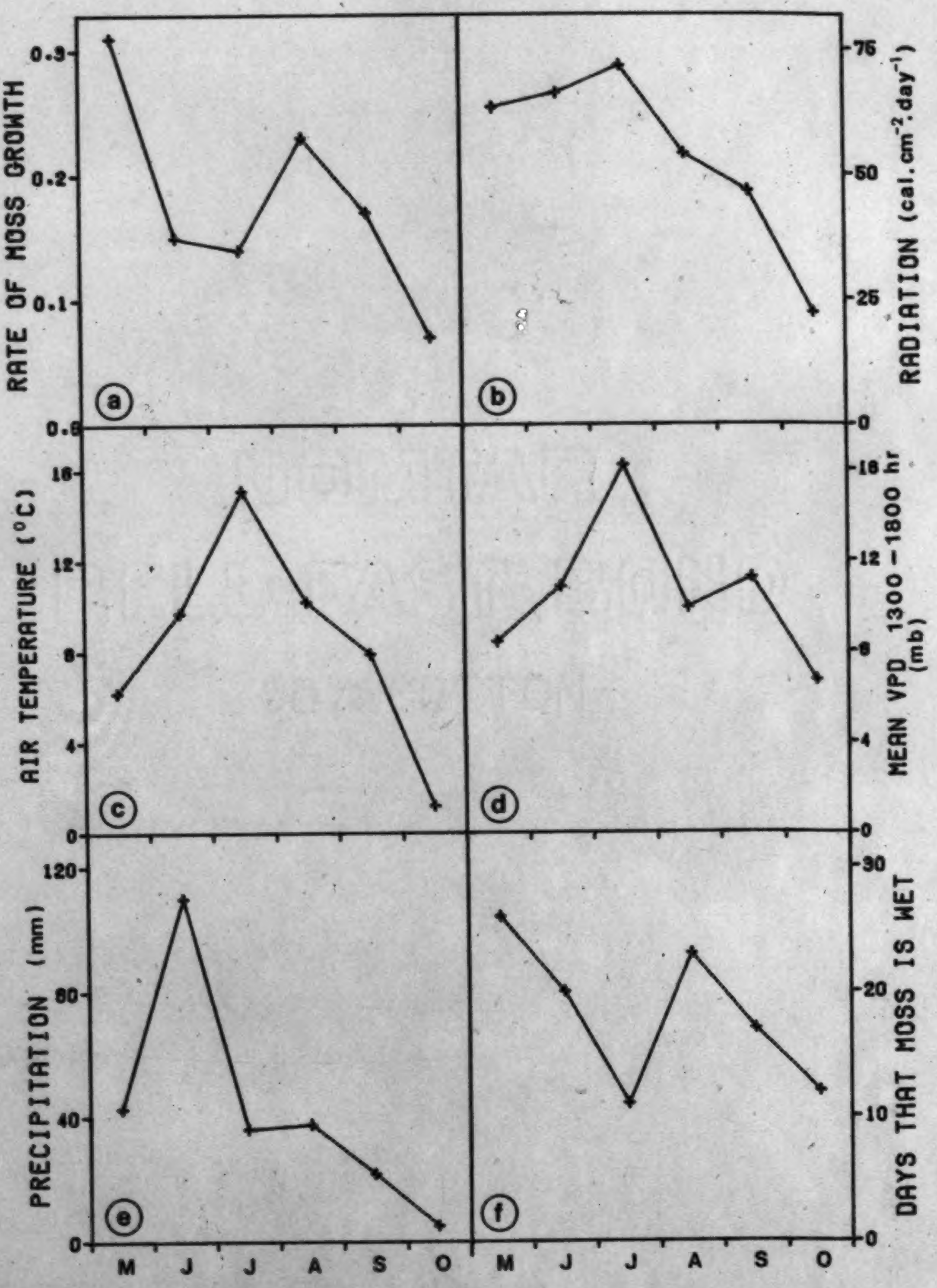

Figure 29. Growth of Hylocomium splendens (relative to 1973 layer) compared with selected environmental factors.

Table 8. Mean length increments for three of the colour categories of Tomenthypnum nitens in 1975 as percentages of total length increments.

	Colour Category			
Month	Green	Yellow-green	Yellow-brown	Mean
May	20	15	10	15
June	33	35	30	33
July	17	20	30	22
August	17	15	20	17
September	13	10	10	11
October	0	5	0	2

only 0.72 and field measurements had shown high apical water contents up to 12 days after rain (see IV.2 above), thus indicating a relative independence of rainfall per se. The influence of rainfall on growth, therefore, must be manifested through storage of water either in the moss canopy or in the ground water table. Canopy water holding capacity depends on stem morphology and density and probably varies somewhat with the variation in canopy morphology noted above (III.4). Since T. nitens has a low resistance to water movement, and assuming that this resistance is more or less constant with depth, it is reasonable to conclude that rate of water movement in the canopy, and hence the canopy water content, is controlled by ground water level

under conditions of constant evaporation stress. Ground water level, therefore, may be important in controlling field growth rates. Additional evidence for this hypothesis was obtained from transplants (discussed below) which showed that growth rates were negligible in habitats where no ground water was available.

During the 1975 season the water level in the fen was measured relative to a metal rod embedded to a depth of about 1.5 m in the peat. The correlation coefficient between weekly variation in water level and rainfall was poor (0.35), but when the correlation between water level variation and precipitation minus estimated weekly evaporation was calculated, the coefficient was 0.65. The evaporation data were obtained from Fig. 12 and additional data for May and June estimated from the water vapour deficits in Fig. 11. Relative to the level at the beginning of May, the mean monthly water levels from May to October were 35,58,86,120,110, and 110 mm lower. The correlation coefficient between these values and average growth was only -0.48. However the ground water was frozen in early May and late September and growth may have been limited at these times by low temperatures and/or water stress due to reduced rates of transport through the canopy. When the May and October values were excluded from the calculations, the coefficient was found to be -0.91. This value was not statistically significant and should be interpreted with caution. The inaccuracies in estimating the growth rates, the complex nature of water level fluctuations and canopy water content fluctuations, and the low number of samples all contribute to difficulties in assessing the reliability of this correlation. It seems reasonable, however, to suggest that, while rainfall is probably the ultimate controlling factor, growth of _T. nitens_ is limited by low temperature at the beginning and end of the season and by increasing depth to the water table during the summer.

If growth of _T. nitens_ was influenced by variation in the ground water level in the fen, then this effect must occur through variation in water content of the moss apices. From the relationship between water content and colour of the apical region, outlined above, it would be expected that the colour of individual stems would change during the season. No attempt was made to monitor colour changes in the field, but examination of field notes provided no evidence that significant changes occurred; samples assigned to a particular colour category near the beginning of the season tended to remain in that category and, when changes were noted, no particular trend was evident.

The correlation coefficient between growth and mean daily global short-wave radiation (monthly means obtained from Fig. 4, p.27) was fairly high (0.84). The light response curve of the growth chamber material (Fig. 20, p.95) showed a "light saturation" of 8000 lux (IV.1.c), which is only about 8% of full sunlight. This material, however, may have been acclimated to the chamber conditions (maximum illumination 16900 lux), so the results may not be applicable to the field. Since this species is exposed to full sunlight in its normal habitat, and since it has either a low light saturation value or can acclimate to lower light intensities, it is unlikely that radiation was a factor limiting growth during the measurement period.

The correlation coefficient between growth and mean monthly air temperature (Fig. 29c) was only 0.70. Apart from the beginning and end of the season when low air and canopy temperatures probably limited growth, variation in air temperature during the season seems not to have been a controlling factor.

Evaporation stress is probably also a factor in determining the water content of the shoot apex; the initiation of new shoots by the brown moss late in the season was probably due to a reduction in evaporation allowing a more favourable water status in the apical region. Additional evidence for this hypothesis comes from observations made in 1975 of material trampled during the 1974 field season. The trampled moss was bright green and had grown some 2-3 cm in an estimated time of 3-4 months, a rate which was considerably faster than normal. This was attributed to the fact that the apex was closer to the water table and was not limited by water stress. If this is so then it is probable that the T. nitens canopy is controlled by the balance between water transport and evaporation and net long-term growth of the canopy is probably controlled by changes in the water table and the decomposition rate. Due to the numerous sources of error in this analysis these conclusions must be regarded as being tentative and subject to confirmation by further studies.

b) _Hylocomium splendens_

This species has a complex phenology (see III.3 above), which makes it difficult to relate growth rate to environment. In 1975 each of the 1974, 1975 and future 1976 layers showed some growth (cf. Tamm 1953, p.27), thus it was necessary to consider all these layers in evaluating the growth rate of the species. The biomass increases of the 1974, 1975 and 1976 layers during each month of the 1975 season, obtained from Fig. 17 (p.74), are shown in Table 9, along with the total biomass increase in each month. Values in Table 9 represent increases relative to the 1973 layer but can be converted to mg by multiplying by 12.8, since the average biomass per stem of the 1973 layer was 12.8±0.11 mg (mean±s.e., n=2038). If Tamm (1953, p.21) is correct in stating that "...growth may be loosely equated with dry matter increase", then the monthly totals for biomass increase can be readily correlated with environmental factors in attempting to elucidate factors which control growth rate.

The assumption which is implicit in this approach is that biomass increase is small compared with the pre-

Table 9. Biomass increase in layers of Hylocomium splendens in 1975 expressed as ratios of the 1973 layer.

Month	1974 Layer	1975 Layer	1976 Layer	Total
	Biomass Increase (Relative to 1973 Layer)			
May	0.26	0.05	0	0.31
June	0.08	0.07	0	0.15
July	0.04	0.10	0	0.14
August	0	0.22	0.01	0.23
September	0	0.16	0.01	0.17
October	0	0.06	0.01	0.07

existing biomass, or "standing crop", and so changes in rate of increase can be attributed mainly to external environmental factors. If each layer of this species, however, is essentially independent of the layers below it, then the biomass increase of each layer should be related to the standing crop of that layer. In this case the relationships between growth and environmental factors would be complicated by phenological factors such as initiation of new layers and senescence of older ones. Tamm (1953, p.60), for example, stated that "In all probability most of the nutrients taken up by Hylocomium splendens are absorbed by the growing organs themselves", and (p.119) that "...of the nutrients and photosynthates used by the young segment in its growth, relatively little is supplied by the parent segment."

If nutritional independence of the layers is assumed, then the growth of the species can be expressed as the monthly biomass increase of each layer relative to the average standing crop of that layer in that month (Table 10). This Table shows that high growth rates were achieved in May, June and August, with intermediate growth rates in July and September and a low growth rate in October (cf. Longton 1972c). These data show a close relationship to the totals in Table 9, and in fact the means in Table 10 show trends identical to the trends in the Table 9 totals (correlation coefficient 0.96). The relative rates of growth in each month, therefore, appear to be similar whether the layers are considered nutritionally independent or not. In the absence of any experimental evidence which could distinguish between these growth models, the monthly totals from Table 9 were used to represent growth of _H. splendens_ in 1975 and are compared in Fig. 29 (p.118) with trends in various environmental parameters.

Comparison of the growth of _Hylocomium splendens_ (Fig. 29a) with mean daily global short-wave radiation (Fig. 29b) shows that the correlation is poor (correlation coefficient 0.50). Some workers have suggested that light may limit Feather moss growth. Tamm (1953, p.41-45) discussed the relationship between light levels and spatial variation in production of _H. splendens_ and concluded

Table 10. Biomass increase in layers of *Hylocomium splendens* in 1975 relative to pre-existing biomass (Standing Crop).

Month	Biomass Increase Relative to Layer "Standing Crop" 1974 Layer	1975 Layer	1976 Layer	Mean
May	0.34	1.11	0	0.48
June	0.09	0.67	0	0.25
July	0.04	0.53	0	0.19
August	0	0.63	0.67	0.43
September	0	0.30	0.40	0.23
October	0	0.09	0.29	0.13

(p.109) that "...there seems to be little doubt that light deficiency limits moss growth beneath a dense canopy..." Tarkhova and Ipatov (1975) experimentally manipulated light levels over a Feather moss canopy and concluded that "The detrimental influence of severe shading [illumination 5-10% of that in open areas] on all species was slight but reliable...", and Weetman and Timmer (1967) noted that "Maximum green moss yield [Feather mosses] is attained beneath a canopy which intercepts about 60% of the total light intensity. At lower light intensities moss growth is lower." Birse (1958b) also implied that light can be limiting in stating that "Species of the Weft form [which includes the Feather mosses] occur where illumination is least reduced by taller plants." On the other hand Pessin (1925) and Barkman (1958, p.171) considered direct effects of illumination to be, in general, of secondary importance in the growth and distribution of epiphytic bryophytes.

In this study radiation levels under the _Picea mariana_ canopy (Fig. 29b) varied from an average of 71.6 cal cm^{-2} day^{-1} in July to 22.2 cal cm^{-2} day^{-1} in October. With a daylight period of 16.4 hr in July and 10.4 hr in October (Environment Canada 1974), these light levels average 0.073 and 0.036 cal cm^{-2} min^{-1} respectively. Van Zinderen Bakker (1974, Appendix F) measured light levels in a _Picea mariana_ forest and my evaluation of his data showed that the relationship between Photosynthetically Active Radiation (PAR, μ Einstein m^{-2} sec^{-1}) and global short-wave radiation (R, cal cm^{-2} min^{-1}) was:

$$\log PAR = 0.979 \log R + 3.109.$$

This equation accounted for 98% of the variance. The light levels of 0.073 and 0.036 cal cm^{-2} min^{-1} correspond to 99.1 and 49.6 μ Einstein m^{-2} sec^{-1}. These values, on comparison with the _H. splendens_ light response curve (Fig. 19, p.94), correspond to net assimilation rates of 2.7 and 2.2 mg CO_2 • g dry wt^{-1} • hr^{-1}. Assuming that growth rate is correlated with net assimilation rate, these data indicate that light is unlikely to be a significant factor in controlling growth rates, even late in the season, since a 69% decrease in average radiation level from July to October would be expected to cause only a 19% decrease in average net assimilation rate, whereas the actual decrease in growth was closer to 50%. If this species is able to adapt to changing light levels (cf. Hosokawa _et al_. 1964, Kallio and Heinonen 1973), then the effects on net assimilation may be even less significant. There is also no apparent relationship between radiation and growth rate in mid-summer. It is unlikely that high radiation levels in June and July would be responsible for depressing the growth rate even though high light levels inhibit net assimilation (Fig. 19, p.94). Even during October the average light level would allow an average net assimilation rate which is 65% of maximum, and this level must be exceeded frequently during the middle of the day.

This analysis of the influence of light intensity on moss growth is, of course, highly simplified and the conclusions must be regarded as tentative until confirmed by more thorough studies.

Comparison of the growth of _H. splendens_ (Fig. 29a) with mean monthly air temperature (Fig. 29c) also shows a very poor correlation (correlation coefficient 0.15). The low growth rates in October might be due, in part, to low temperature (cf. Tallis 1959, 1964), however low temperatures may be advantageous because there is evidence that respiration rate is lowered more than photosynthesis (Tamm 1953, p.102). Other workers have also stated that air temperature appears to have little direct influence on bryophyte growth (e.g. Pessin 1925; Barkman 1958, p.171;

Pitkin 1975). Responses of net assimilation rate to temperature were not measured in this study, but the results of other studies, for example Stålfelt (1937a), and the poor correlation between temperature and growth, indicate that air temperature, per se, is not a significant factor in limiting growth.

Comparison of the growth of H. splendens with mean vapour pressure deficit (VPD) at 1300-1800 hr (Fig. 29d) shows a correlation coefficient of -0.76 from May to September, but this coefficient falls to -0.09 when data from October are added. As Barkman (1958, p.69) noted, water loss and supply (except precipitation) depend on VPD and this factor has been considered by many workers to be extremely important in controlling bryophyte growth and distribution, for example Pessin (1925) and Clausen (1964). Tallis (1959) considered that Rhacomitrium lanuginosum is confined to areas with oceanic climates because of deleterious effects of low humidities (see also Kallio and Heinonen 1973). It seems probable that high VPDs are at least partially responsible for limiting growth of H. splendens in mid-summer.

Comparison of the growth of H. splendens with total monthly precipitation (Fig. 29e) shows a poor correlation (correlation coefficient 0.16). Other workers, for example Tamm (1953, p.47,110), Barkman (1958, p.64,171) and Pitkin (1975), have stated that growth of mosses in dry habitats is not controlled by absolute amounts of precipitation; however they did indicate that intensity and, particularly, frequency of rainfall are very important. This is significant because, as Tamm (1953, p.48) pointed out, "The really important thing is probably the time when the moss carpet is wet enough to photosynthesize."

In the present study an attempt was made to estimate the number of days in each month during which the moss was wet enough to photosynthesize. For each month the number of days in which rainfall exceeded 1 mm was noted. It was assumed that rainfall of less than 1 mm was completely intercepted by the tree canopy (see II.3 above).

Samples collected during June and July in 1974 and 1975 showed that moss apical water contents declined to 0.15±0.011 g • g dry wt^{-1} (mean±s.e., n=9) within three days after rain (cf. Stålfelt 1937b). At these values the water potentials of the moss apices were in equilibrium with the water potential of the air above them[1] (cf. Hosokawa et al. 1964, Willis 1964), and it is apparent from Fig. 21 (p.98) that net assimilation would have ceased by this time.

Monthly totals of "moss wet" days were estimated assuming that the moss was wet enough for net assimilation to take place for two days following precipitation in mid-summer, and three days following precipitation from mid-August to October (to allow for reduced evaporation). These totals are presented in Fig. 29f which shows that the relationship between estimated number of days that the moss is wet and growth rate is very close (correlation coefficient 0.88). Pitkin (1975) also reported a high correlation between "rainfall minus potential evapotranspiration" (considered to be closely related to the length of time which the mosses were wet) and growth (see also Proctor 1972). Moss growth in June is lower than might be expected, but this can be attributed to cessation of growth of the 1974 layer and the early stages of growth of the 1975 layer. In fact the rate of biomass increase of the 1975 layer was quite high in June (Table 10).

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[1] Water potential of the air [assuming a diurnal temperature range of 5-22°C (Fig. 6) and a relative humidity range of 83-45% (section II.3)] varies from about −240 to −1100 bar. From Fig. 25 these values are equivalent to moss water contents of 0.12-0.26 g • g dry wt^{-1}.

The correlation coefficient between monthly precipitation and estimated number of days that the moss was wet was only 0.38 so, contrary to the assumption by Tamm (1953, p.48), the former cannot necessarily be used to estimate the latter.

Growth rates of *Pleurozium schreberi* and *Ptilium crista-castrensis* in 1975 were not measured. The responses of these species to the various factors are assumed to be similar to those of *Hylocomium splendens*.

4. Microclimate and Bryophyte Distribution

a) Tomenthypnum nitens

Some of the factors which control the growth rate of this species were outlined in a previous section. The most important parameter appears to be the balance between water transport to the apex and evaporation stress. The habitat limits of the species, therefore, would be expected to be correlated with changes in this parameter great enough to inhibit growth.

Factors which may prevent growth in very wet habitats, for example flarks (see II.2 above), were not investigated. Birse (1958a) reported that species with a growth form similar to T. nitens were adversely affected by long periods of submergence, but the nature of this effect was not established.

Factors which inhibit invasion into habitats occupied by the Feather moss species were investigated using reciprocal transplants. Mats of T. nitens, each about 30x55 cm, were moved to the "Feather moss transplant site" (site 4, Fig. 2, p.15) on 14 May 1975. At the same time a mat was also transplanted to the "Ridge-crest transplant site" (site 5, Fig. 2). In addition cross transplants were made within the fen to determine the effect of the transplant process itself. During subsequent monitoring of the transplants during the rest of the 1975 season, no adverse effects attributable to transplanting alone were detected.

It was found that Tomenthypnum nitens was able to survive and even grow in the Feather moss habitat, and in fact isolated stems are common in the wetter regions under normal conditions (see II.2 above). Growth rates, as measured by cranked wires (see III.2 above), however, were only 20-40% of rates achieved in the natural habitat.

The mat transplanted to the ridge crest showed no growth at all during the season. One week after transplanting, the moss appeared browner than comparable material in the fen and after two weeks the mat was uniformly brown (Plate 3a, p.70). Periods of rain and reduced evaporation promoted some recovery, at least around the edge of the mat in sheltered locations, but the moss in this habitat appeared more adversely affected than any other transplant. It did, however, remain alive; samples brought into the laboratory and kept moist for a few days showed positive net assimilation.

The major difference between the normal habitat of T. nitens and the ridge-crest is that ground water is present in the fen but is not available on the ridge crest. Birse (1958a) noted that species with growth forms similar to T. nitens were "constantly within reach of the water table" in their normal habitat and, when transplanted, their condition deteriorated and they turned brown. Some recovery in autumn was noted, presumably, as in this case, during conditions of higher precipitation and lower evaporation.

In the present study the moss transplanted to the Feather moss habitat did not deteriorate, although the growth rate was reduced. This is probably due to the fact that the evaporation rate at the forested Feather moss site was lower than in the open. In Birse's study the Feather moss site was not forested and evaporation rates at each location were found to be similar.

Tomenthypnum nitens, therefore, appears to be limited by evaporation stress in habitats where ground water is not available. The requirement for ground water does not appear to be compensated for by rainfall, even in habitats where the evaporation stress is lower than in the natural habitat. Whether this is due to the comparatively low water holding capacity of the stems (IV.1.c), to downward movement of water away from the apical region via the tomentum, or to some other factor, is not known.

Although this species can survive in habitats occupied by Feather mosses, its growth rate is reduced and it would probably be overtopped and out-competed by the Feather mosses under normal conditions. Its maximum net assimilation rates appear to be lower than the Feather mosses' (compare Fig. 24 with Figs. 21 to 23) and its desiccation tolerance may also be lower. Abel (1956) showed that the desiccation resistance of Aulacomnium palustre, a species which occupies habitats intermediate between those of T. nitens and the Feather mosses (Appendix I, see also Vitt and Hamilton 1975), is lower than that of the Feather mosses. If this is also the case with T. nitens, then its fitness in the Feather moss habitat would be even lower.

b) Feather mosses

Transplants were also used to determine the nature of the habitat limits of the Feather mosses. On 14 May 1975, mats of Feather moss, each about 30x55 cm, were transplanted to the "Tomenthyrnum transplant site" (Plate 4a and site 3, Fig. 2). At the same time a mat of Feather moss was transplanted to the Ridge-crest transplant site. In addition cross transplants were made within the Feather moss community and, as with Tomenthyrnum nitens, no adverse effects attributable to transplanting were detected.

Feather mosses transplanted into the fen showed signs of damage when examined one week later. Some of the more exposed individuals appeared bleached (Plate 4b), perhaps a symptom of radiaticn damage (see IV.1.c above). After two weeks much of the canopy surface was bleached, some stems appearing almost white. Ptilium crista-castrensis appeared to be more damaged than Hylocomium splendens, and Pleurozium schreberi appeared least affected. This is consistent with observations by Birse (1957) that P. schreberi is more "phototrophic" than H. splendens (see also Tamm 1953, p.46,103). Individual stems in sheltered locations around the periphery of the transplants appeared undamaged. Over the next three months the condition of the transplanted

Plate 4

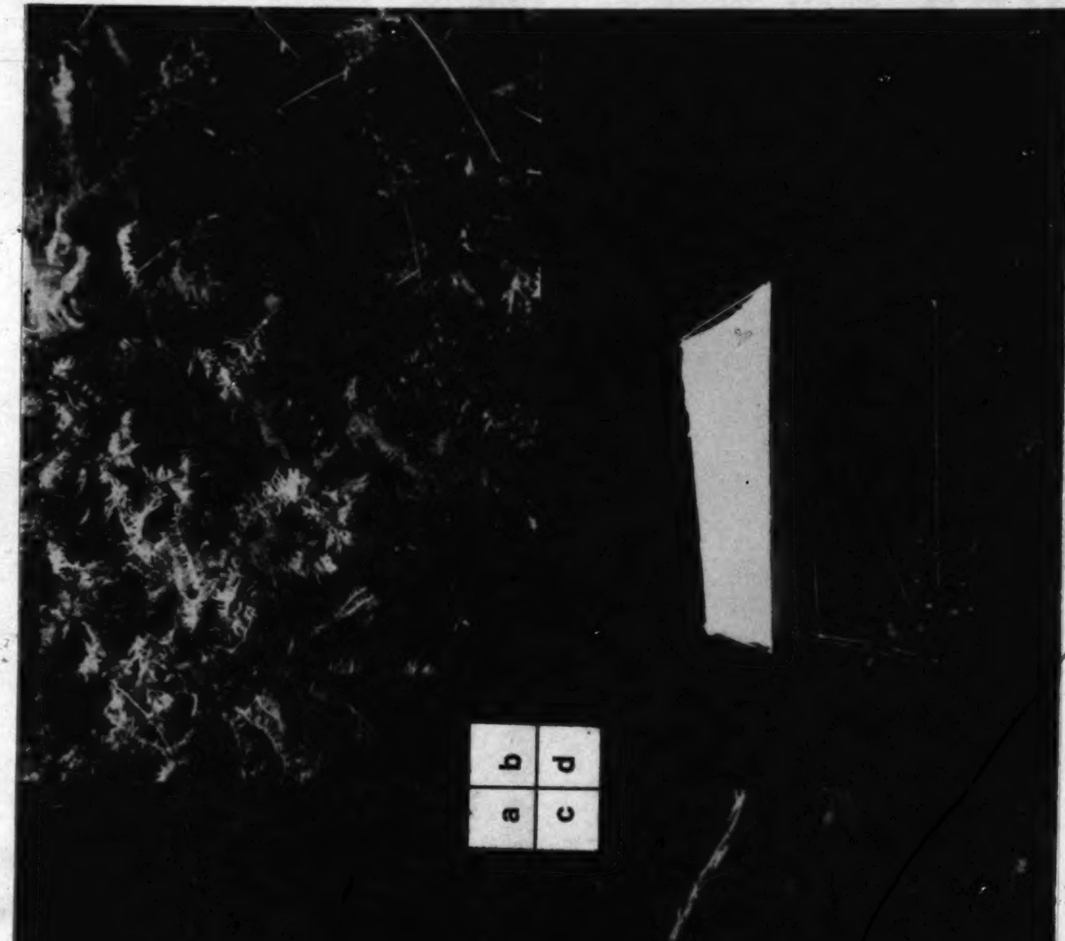
Feather moss transplant experiments:

a) Feather moss mat freshly transplanted to *Tomenthypnum* habitat. Size of transplant is approximately 30 x 55 cm.

b) *Ptilium crista-castrensis* transplanted 14 May, photographed 28 May. Note severe bleaching of exposed stems while protected stems remain green. Brown moss in foreground is *Tomenthypnum nitens*.

c) Feather moss mat transplanted to *Tomenthypnum* habitat on 14 May, photographed 27 August. Most stems show new growth.

d) Shade experiment on Feather moss transplanted to *Tomenthypnum* habitat. Note that, while all of transplant is shaded from solar radiation, half is sheltered from, and half exposed to precipitation.


a
b
c
d

Feather mosses continued to deteriorate until most of the visible material, except for that in sheltered locations, appeared dead. Towards the end of August, however, there appeared to be some recovery, probably due to the overcast, showery weather which prevailed for much of that month. Some of the less damaged material appeared to recover and new green shoots emerged from many of the remaining stems (Plate 4c). By the end of October about one-third of the transplanted material was green or showed new growth.

Feather mosses, therefore, appeared to be damaged by conditions associated with the period from May to mid-August. Factors which could have contributed to the deterioration of the Feather mosses during this period are radiation, temperature and evaporation stress. To test the effect of radiation, a fresh mat of Feather moss was transplanted into the fen on 9 July 1975 and shaded by a cheesecloth screen designed to reduce the radiation to 20% of incident, i.e. similar to the normal Feather moss habitat (Plate 4d). To compensate for the sun angle, the screen was set up so that, although all the moss was screened from direct radiation for most of the day, only half was covered by vertical projection of the screen, the other half being exposed to the sky. This meant that half of the moss mat was somewhat sheltered from rain while the other half was exposed to normal precipitation. The mat was monitored for the next three weeks and the condition of the moss appeared to slowly deteriorate, especially the half which received little or no rain. Rain thus appeared to be essential in maintaining the moss in a healthy condition. Deterioration, however, was not as rapid as in the fully exposed material, indicating that direct and indirect (i.e. temperature) effects of radiation were indeed contributing factors. Higher evaporation stress in the more open habitat compared with the normal habitat under the tree canopy probably accounted for the damage to the shaded material.

The effect of evaporation was tested by monitoring the condition of a Feather moss mat transplanted into the fen on 11 June 1975 and covered by a plexiglass box. The aim was to reduce the evaporation stress to determine if this improved the viability of Feather moss in the open fen environment. The box, however, prevented precipitation from reaching the moss and probably also caused a considerable temperature elevation, although this was not measured. The condition of the Feather moss mat deteriorated so rapidly that, within two weeks, it appeared in worse condition than the exposed transplants after six weeks. The deleterious effects of radiation, isolation from precipitation, and presumed high temperature, completely overwhelmed any possible beneficial effects of evaporation reduction.

So far discussion has centred on Feather moss mats transplanted so that the canopy surface was level with the surrounding _Tomenthypnum_ _nitens_. Since the Feather mosses have a higher resistance to external water movement than _T. nitens_ (see IV.2 above), most of the transplants so far discussed were not maintained in a moist state by ground water from the fen, except around the edges, but were wetted only by precipitation. Mats of the Feather mosses, therefore, were transplanted into the fen and placed so that the ground water was able to move freely to the tops of the canopies. Within two weeks the tips of the branches and shoot apices had turned black. The same phenomenon has been observed in the growth chamber when mosses were maintained in poorly drained conditions and not protected from evaporation stress. When some of these black tips were examined it was found that the colour was due to a deposit among the leaves. The deposit could be rinsed out with water and, when diluted, it was similar in colour to water taken from the trays in which the moss was growing in the growth chamber. It also stained similarly with Toluidine Blue. It is suggested that this material was transported up the stems in the water stream and was deposited at the shoot tips as the water evaporated. It is not known why this phenomenon does not occur in _T. nitens_; perhaps the rhizoids of the tomentum filter the material out of the water as it moves up the stems. Growth of the Feather mosses, therefore, appears to be inhibited when water is supplied from below, at least in conditions of high evaporation stress. This is in agreement with observations by Birse (1958a) on the adverse effect of high water tables on Feather mosses.

An additional explanation for the inhibition of Feather moss growth in the fen is depression of net assimilation at high water contents (Figs. 21 to 23) [see also comments on Rhacomitrium lanuginosum by Tallis (1959, 1964)]. This, along with the other factors, may place the Feather moss species at a competitive disadvantage with respect to the fen species and prevent their colonization of this habitat.

The Feather moss species, therefore, appear to be limited in the fen habitat by an interacting complex of factors including radiation damage and evaporation stress (cf. Tamm 1953, p. 104). Factors associated with high water tables, for example formation of black deposits and depression of net assimilation at high water contents, would probably inhibit initial colonization (cf. Gimingham and Brynard 1959), but would be expected to gradually lose their influence (if the moss could become established) as canopy growth proceeded. There are insufficient data at present to distinguish between these and other factors, and to determine which are fundamentally limiting and which could be overcome by appropriate adaptations.

The Feather moss mat transplanted to the ridge crest on 14 May showed some signs of damage one week later; some of the stems of Ptilium crista-castrensis appeared slightly bleached. The condition of the mosses deteriorated during the following three months, but this deterioration was not as severe as in the material transplanted into the fen. Measurements with an actinograph indicated that the trees around the ridge top site reduced the incoming short-wave radiation to about 60% of that recorded at the *Tomenthypnum* site, so the reduced severity of the damage may be attributable to lower radiation levels. From mid-August to early September, again correlated with overcast showery weather, there was considerable recovery, but after that time exposure on the open ridge and low precipitation appeared to cause further deterioration.

In the area around the ridge-crest transplants *Pleurozium schreberi* and some *Hylocomium splendens* occur underneath the dwarf-shrub species *Vaccinium vitis-idaea* var. *minus* and *Arctostaphylos uva-ursi* which have a cover of nearly 100% in the area. At least these two species, therefore, can survive in this habitat if protected by a shrub canopy. It appears, therefore, that radiation and evaporation stress limit the Feather moss species in dry, non-forested habitats. Feather moss species are, however, not restricted to forests. Tamm (1953, p.45), Birse (1958a,b) and Watson (1960) report that Feather mosses commonly occur in protected, non-forested areas, particularly on north-facing slopes. Beil (1966) performed a multiple regression analysis of bryophyte cover (chiefly Feather mosses) in subalpine spruce-fir forest and concluded that "The development of the terrestrial bryophyte-lichen stratum appears to be independent of environment created by the tree stratum. Environmental variables manifested through elevation and aspect are of prime importance." These studies suggest that Feather mosses grow in forested tats primarily because of the protection from ration stress and that any chemical or biotic action with the tree species, such as nutrient supply llelopathic effects, are probably of secondary rtance.

Feather moss growth also appears to be limited in some s within the forest. There are frequently areas, with i of 20-40 cm, around the bases of Picea mariana trees h are clear of mosses, and other vegetation. Moss yield nown to decrease from the edge of the tree canopy ards the trunk, and this has been variously attributed to itation by low light (Tamm 1953, pp.41-46,109), ibiting effects of litter fall (Tarkhova and Ipatov 5), and insufficient precipitation (Abolin' 1974).

Levels of radiation incident on a clear area at a tree e and on a nearby mat of Feather moss were measured for week with actinographs. No significant differences ld be detected. The role of litter in limiting moss wth is difficult to determine and no doubt varies siderably with forest type. Tamm (1953, pp.105-106) cated that litter fall can be limiting, but only when th is already reduced by light deficiency, and LaRoi and nger (1976) state that a Feather moss stem "...can pass ugh or thrust aside a surprisingly thick layer of itus." Indications are, therefore, that the absence of her mosses around the bases of trees is not due rily to detritus limitation or low light levels.

[redacted]

The other factor thought to inhibit growth of Feather mosses near the bases of trees is water limitation. Field observations indicated that the canopy morphology of *Picea mariana* tends to re-distribute precipitation so that it tends to flow to the ends of the branches and fall in the drip zone around the canopy periphery. Stem flow in conifers is generally considered to be negligible (Geiger 1966, p.331; Weetman and Timmer 1976; LaRoi and Stringer 1976). In this study "Tru-Chek" rain gauges were placed on the clear areas and the precipitation collected was compared with that recorded at nearby locations above Feather mosses. The measurements indicated that showers of less than 5 mm (in the open) did not penetrate through to these clear areas in measureable amounts. If rainfall in the open was more than 5 mm, then from 2-27% (average 14% for 10 readings) penetrated to the clear areas. This compares with an average penetration of 78% for the Feather mosses (see II.3 above). Maximum moss production seems to occur in or near the drip zone (Tamm 1953, p.41; 1964; Abolin' 1974) so it is probable, therefore, that water supply is responsible for limiting growth of Feather mosses underneath tree canopies, particularly at tree bases.

V. DISCUSSION

Many of the problems in the ecology of these species, and of bryophytes generally, require understanding of the physiological and biochemical processes involved in tolerance of and recovery from desiccation. Recent research has indicated that:

> "The rate of recovery of photosynthesis on re-moistening, the rate of decline of the limiting photosynthetic rate following progressively increasing desiccation, the cause of the initial stimulation of respiration and of the longer-term build-up of respiration after more prolonged desiccation, and the reasons for the death of bryophytes after desiccation damage, all require substantially independent explanations" (Dilks and Proctor 1974).

The rate of recovery on re-moistening was not investigated in this study, but studies on Hylocomium splendens by Stålfelt (1937a) and Dilks and Proctor (1974) have shown that recovery rate decreases with increasing duration of desiccation. Vitality of the moss, however, does not appear to be significantly affected by dry periods of less than about 40 days. Since dry periods at the study site in excess of this amount appear to be infrequent, deleterious effects on this species of long periods of desiccation are probably rare (cf. Hinshiri and Proctor 1971). The other Feather moss species are probably comparable in their tolerance to desiccation but no information is yet available.

Dry periods in the order of 10-15 days during mid-summer, however, could reduce the amount of Feather moss growth during subsequent wet periods if recovery from desiccation takes a significant proportion of the time available for photosynthesis. Available time is limited by high evaporation rates to two or three days following rain during this period and, if local areas of moss are exposed to radiation penetrating through gaps in the tree canopy, this time may be even further reduced. This effect would augment the influence of initial variation in water contents caused by interception and redistribution of precipitation by the tree canopy. Also if some of the moss stems were unable to recover completely from the previous dry period before drying out again, then the effect of the two desiccation periods may be cumulative, thus reducing recovery rate even further on subsequent rehydration (see also Tallis 1959, Proctor 1972). This would reduce the growth of these stems in comparison to those which had completely recovered in the intervening wet period. Differential desiccation rates, along with spatial variation in rainfall under the tree canopy, are no doubt responsible for the considerable variation in water content and growth rate noted in the field (see also Tamm 1953, 1964; Klepper 1963; Lee and Stewart 1971; Abolin' 1974).

In the case of Tomenthypnum nitens, duration of dry periods would be expected to have little direct effect since ground water is probably available for most of the season. In direct contrast with the Feather mosses it appears that the total amount of precipitation, rather than frequency or intensity, controls the growth rate of this species through its influence on the ground water level. The relationship between precipitation and ground-water level, however, is complicated by factors such as evaporation rate and drainage from the fen system, and the relationship between ground-water level and moss growth rate is further complicated by swelling and shrinking of the moss canopy with variation in water status (see Sonesson and Johansson 1973), relative decomposition rates, and the influence of evaporation on apical water contents. Confirmation of the hypothesis that total precipitation controls the growth rate of this species would require more accurate measurement of the very slow growth rates and evaluation of the significance of the various complicating factors.

The rates of decline of net assimilation with progressively increasing desiccation appeared to be similar among the four species studied. Both photosynthesis and respiration decreased with increasing desiccation but photosynthesis appeared to be more severely affected since, in all species except Pleurozium schreberi, respiration was detected after photosynthesis had apparently ceased (cf. Mayer and Plantefol 1926 and Plantefol 1927, both cited in Patterson 1943). In the Feather moss species net photosynthesis probably ceases or becomes negative at water contents below 0.4 g • g dry wt^{-1}, so no growth is likely when water contents reach equilibrium with the water potential of the air at 0.12-0.26 g • g dry wt^{-1}. Experiments indicated that moss stems have a negligible resistance to water loss and that water loss tends to be linear with time, at least until water contents are very low (cf. Barkman 1958, p.81; Klepper 1968; Hoffman and Gates 1970). This means that mosses in the field dry out so rapidly that differences between the species in the effect of desiccation on net assimilation rate would be unlikely to significantly influence relative growth rates.

A burst of respiration occurs on wetting after even short periods of desiccation. It is apparently not linked specifically with the recovery of photosynthesis because it has been observed after periods of desiccation long enough to destroy any capability for recovery (Dilks and Proctor 1974). Bewley and Thorpe (1974) stated that the respiration burst in Tortula ruralis apparently reflected increased glycolytic activity; however Bewley and Gwóźdź (1975) noted that ATP levels remained constant and suggested that either the respiration burst is uncoupled from ATP production or ATP is synthesized but used at a rapid rate. Tucker et al. (1975) investigated ultrastructural changes that occurred in T. ruralis upon rehydration and showed that, 2-5 min after wetting, considerable organelle disruption was apparent, mitochondria and chloroplasts being swollen and distorted. They suggested that the respiration burst might be correlated with repair of this damage. Addition of liquid water to desiccated moss has long been considered injurious (for example Abel 1956), but Levitt (1972, pp.342-344), noting the variation in experimental results, concluded that the situation was far from clear. Tucker et al. (1975) suggested that "...the ability to withstand desiccation lies not in the ability of the protoplasm to remain unchanged during dehydration and rehydration but in the ability of the protoplasm to return to what we consider as a unstressed condition."

Desiccation tolerance has been shown to vary with season (Ochi 1952, Hinshiri and Proctor 1971, Lee and Stewart 1971) and this variation has been correlated with variation in osmotic potential (Hosokawa et al. 1964). Patterson (1964) also noted this correlation but commented that the influence of osmotic potential on xerophytism was still an open question.

In addition to seasonal variation there may also be a gradient in desiccation tolerance within individual stems (Abel 1956) since, in some species, young leaves have been shown to be more tolerant to desiccation than older leaves (Hinshiri and Proctor 1971). Differential tolerance may explain the ability of some species to recover after severe stress. Dilks and Proctor (1974), for example, reported that a small proportion of the shoots of Hylocomium splendens survived prolonged desiccation, and it was noted in the present study that new shoots developed in the transplanted Feather mosses and in the brown coloured Tomenthypnum nitens during favourable conditions in late-

August 1975. Whether these new shoots were more stress tolerant or merely better protected was not established. Differential desiccation tolerances and differences in ability to adapt to desiccation stress (cf. Abel 1956) are probably significant factors in controlling relative distributions of bryophytes, but insufficient information is presently available to elaborate on this.

It has been shown in this study that water has a major influence in controlling growth rates and in determining habitat limits of the species examined. Water movement however is apparently not under biological control since there appear to be no significant differences in water absorption (Müller 1909, cited in Anderson and Bordeau 1955) or water loss (Stocker 1956, cited in Anderson 1974) between living and dead plants. Barkman (1958, p.81,85) claimed that rate of uptake and capacity to hold water are correlated with habitat, but this is disputed by Patterson (1943) and Anderson (1974). It is important, however, to distinguish between the water relations of individual stems and those of the moss canopy as a unit since, as Gimingham (1967) pointed out, "...it is particularly important in mosses to take into account not only the properties of the individual shoots in respect of water uptake and loss, but also the effect of the way in which the shoots are grouped together in the colony: that is the growth form of the moss."

Bryophytes with similar growth forms occupy similar habitats which suggests that they are responding in a similar fashion to the various environmental parameters in those habitats (Hamilton 1953; Seim et al. 1955; Gimingham and Birse 1957; Birse 1957, 1958a,b). Morphologically, Tomenthypnum nitens would be classified as a "Tall turf with divergent branches of limited growth" along with many of the species of Sphagnum (Gimingham and Birse 1957) and one of the characteristic features of this group is that "...the aggregated shoots act as a wick, drawing water up the exterior of the stems in the small spaces between leaves and stems and between adjacent shoots" (Gimingham and Birse 1957). Growth form is very important in the water balance of T. nitens because its growth appears to depend on the balance between water transport up through the canopy and loss through evaporation; the high density of shoots minimizes loss of water from the stems. Were it not for this protection from evaporation, water transport to the apex would be reduced, thus lowering apical water contents, net assimilation rates and, presumably, the ability of the species to survive and compete in this habitat.

A high shoot density would not be particularly advantageous to the Feather mosses. These species do not depend upon, and in fact appear to be damaged by, water supply from below, so protection from water loss from within the canopy is not necessary. The mosses are subjected to periodic desiccation and, after wetting, the water content of the apical region must remain high for long enough to recover from the effects of desiccation and then to achieve sufficient production to compete effectively against other species. It is important, therefore, that the apex be protected from evaporation stress for as long as possible after rain and this is best achieved in shaded habitats or in environments with high humidity and consistent cloud cover. Species with the ability to recover rapidly from desiccation and with low growth rates, for example Tortula ruralis (Bewley and Thorpe 1974), can survive in more exposed habitats. The Feather mosses, however, appear to be adversely affected by high evaporation stress and the clearing experiments showed that growth rate can be measurably reduced by the removal of a sparse shrub canopy, even in a forested, relatively sheltered site. Since humidity and cloud cover are generally low, evaporation stress in the open is very high at the study site and the Feather mosses are consequently restricted to areas sheltered by trees and shrubs.

One feature which could have some significance in the water relations of bryophytes is the "wettability" of the stems and capacity to hold water after rain. Barkman (1958, p.81) noted that water absorption is very rapid: in xerophytic bryophytes, seconds; less xerophytic bryophytes, 0.5-1 min; mesophytic species, 5-15 min; and hygrophytic species, 1-several hours. Barkman also stated (p.85) that hygrophytic bryophytes have low water holding capacities (5-8 g • g dry wt^{-1}), while most xerophytes have capacities ranging from 9-17 g • g dry wt^{-1}. However, Anderson (1974) claimed that no consistent relationship between water holding capacity and habitat had been found.

The three Feather mosses were shown to have a higher water holding capacity than Tomenthypnum nitens and the significance of this could lie in the fact that growth of the former requires the maintenance of a high water content for as long as possible after rain. The fact that 80-90% of the water in saturated moss is held externally is important because the water content can decrease to 10-20% of the saturation value before any water stress is experienced by the photosynthetic cells. The fact that net assimilation is inhibited at high water contents would not necessarily be a problem in the field since saturation frequently occurs after a previous dry period, and the delay in resumption of photosynthesis would allow some of the excess water to evaporate before photosynthesis commenced. In fact excess water may be advantageous because, by increasing the resistance to carbon dioxide diffusion, it would tend to retain in the apical region the carbon dioxide released by the initial respiration burst and this would then be available for photosynthesis when recovery occurred.

In the case of Tomenthypnum nitens a high water holding capacity would not be advantageous. Unlike the situation with the Feather mosses, rainwater appears to have little direct physiological importance since it is either transported down to the water table or rapidly lost through evaporation. Growth rate in T. nitens is controlled by water supplied from below, and growth is only possible when the rate of transport through the canopy equals or exceeds rate of loss through evaporation. Capillary water in the apical region in excess of metabolic requirements would be deleterious because of the increased resistance to gas exchange. There would be no selective pressure to increase water holding capacity because, with the high evaporation rates in the fen habitat, species with a higher capacity would be unlikely to gain any significant advantage after rainfall over those with lower capacities.

The correlation between water holding capacity and habitat noted by Barkman (1958), therefore, appears to apply to the species examined in this study and may well be applicable to many other bryophytes. Each species, however, should be evaluated individually and conclusions drawn with care because the role of water in bryophyte ecology is complex and involves many parameters, including water source, path of movement through the canopy, rate of loss and frequency of wetting and drying. The morphology of individual stems and the growth form of bryophyte canopies may be closely integrated with the water relations of the species concerned, and further studies in this area may well result in explanations for many of these correlations.

Solar radiation is also a parameter with complex direct and indirect effects. High radiation levels apparently have a direct deleterious effect on feather mosses, but do not appear to affect Tomenthypnum nitens, or at least not to the same extent. Susceptibility to direct radiation damage, however, is unlikely to be a primary factor in limiting Feather moss distribution. This conclusion is based on the fact that these mosses occur in habitats at the study site where they are exposed to radiation levels in the order of 250% of average levels under the tree canopy. They are presumably adapted to these higher light levels and their ability to survive there is possibly due to protection from wind by surrounding trees and shrubs and the maintenance of a high humidity (suspected but not measured) by small pools of water in the area thus reducing evaporation stress to a tolerable level.

There was no indication that low light levels inhibited growth of any of the moss species at the study site during the snow-free season. This conclusion, based on a fairly superficial laboratory study and extrapolation of the results to the field, must be regarded as tentative until confirmed by more thorough studies. However many mosses have been shown to adapt to very low light levels (Hosokawa et al. 1964), and field measurements in the present study suggest that interception of rainfall by dense tree canopies is likely to be more significant than light interception.

Radiation also affects parameters such as air and moss temperature, vapour pressure deficit and local wind currents. Temperature of mosses such as Tomenthypnum nitens in open habitats can show diurnal variations from below 0°C to above 40°C with rates of change exceeding 10°C in 30 min. The actual temperature values are unlikely to be significant since most mosses appear to maintain positive net assimilation rates over a wide range of temperatures, but it is essential to study the effect of rapid temperature fluctuations before any sound conclusions can be drawn. Low temperatures are probably not a hazard to most moss species since water loss from the thin leaves is so rapid that freezing injury due to intracellular ice formation is unlikely to occur (Dilks and Proctor 1975). Tomenthypnum nitens, however, is almost continuously moist and, since canopy temperatures generally drop below air temperature in the early morning, this species can be subjected to freezing temperatures at any time of the season. Net assimilation rates were probably limited at the beginning and end of the season by low temperature and/or water stress due to freezing of the ground water, but the effect of freezing temperature on net assimilation in this species has not been studied. The Feather moss species appear to be relatively unaffected by temperatures as low as -10°C when wet and may survive even lower temperatures in a "freeze-dried" state (Kallio and Heinonen 1973, Dilks and Proctor 1975).

Evaporation stress, which is a function of radiation, air temperature and wind, is an important factor controlling the water balance of Tomenthypnum nitens. In conjunction with rainfall frequency, it is also important in determining the length of time in which the Feather mosses are able to photosynthesize. The restriction of T. nitens to areas with high water tables and the absence of Feather mosses from open, exposed habitats are probably due largely to the effects of evaporation stress.

Other environmental factors such as carbon dioxide concentration near the soil surface, nutrient balance, and impact of grazing were not examined. Carbon dioxide concentration may affect absolute productivity rates but is unlikely to have a significant effect on determining the habitat limits of the species (cf. Tamm 1953, p.101).

The role of nutrients in bryophyte ecology is very poorly understood. The distributions of many species have been correlated with nutrient concentrations but cause/effect relationships are far from clear. Mosses are known to accumulate minerals beyond concentrations found in the substrate (e.g. Tamm 1953, 1964; Anderson 1974), and it has been argued that nutrients frequently limit moss growth (Tamm 1953, p.111; Kallio and Karenlampi 1973). Addition of nutrients to moss canopies in the field has reportedly stimulated growth (Clarke et al. 1971, Kallio and Heinonen 1973, Kallio and Karenlampi 1973), and field observations in this study suggest that animal droppings may stimulate growth of T. nitens. Moss in the immediate area of such droppings had apices which were much greener than the rest of the carpet. This suggests that nutrients may indeed be limiting, at least in some cases, but further studies of nutrient budgets in the field, combined with laboratory experiments, are necessary.

A number of arthropod groups are known to feed on bryophyte gametophytes (Gerson 1969), but the influence of grazing is generally considered to be minor (e.g. Barkman 1958, p.171). Tamm (1953, p.107) noted that "For most animals *Hylocomium splendens* seems to be little if at all palatable and seldom eaten." No evidence of grazing damage was noted in any specimens collected during the present study.

The influence of internal factors on growth regulation in the field is also poorly understood. Growth is considered to be controlled primarily by external factors (Tamm 1953, p.20,37,117; Tallis 1959; Pitkin 1975) but, in species such as *Hylocomium splendens*, internal factors also appear to be involved. In *H. splendens* the bud which will develop into the following year's growth layer is formed at the same time that the lateral branches are initiated in the current year's layer, but its growth is somehow suppressed. This suppression does not appear to require cold treatment for removal, since buds show apparently normal development in material brought into the growth chamber late in the season and kept at temperatures above freezing. Photoperiod also seems not to be a factor since a small proportion of buds showed some elongation in late-September and October, whereas development does not usually take place until the following May or June. It appears that the bud does not start to elongate until the previous segment has completed its growth. If this growth is delayed, for example by removal of the protective shrub canopy, then the development of the bud in the following year also appears to be delayed. This suggests that some form of hormonal balance may be involved, perhaps some kind of apical dominance phenomenon. The segments of the moss may be adapted to reaching a certain size before the inhibition is released and growth of the next layer commences (see also Tamm 1953, p.23,112). One reason for the monopodial growth of arctic and alpine populations of H. splendens (D.H. Vitt, pers. comm.) is possibly that growth rates are lower and development of the lateral bud may be always suppressed. This hypothesis could be tested in the field by removing the apical bud and observing whether sympodial growth resulted.

Many bryophytes show proncunced phenotypic plasticity (Tallis 1959; Forman 1964; Longton 1974a,b) and morphological variation is frequently associated with physiological differences (Bazzaz et al. 1970, Lee and Stewart 1971, Kallio and Heinonen 1973). Whether this variation is genetically determined, a plastic response to habitat conditions, or both, remains to be established in most cases. Szweykowski and Vogel (1966, cited in Anderson 1974) found that North American and European populations of the variable Geocalyx graveolens were identical when grown under the same conditions; however Longton (1974b) found that the variation in growth and morphology of populations of Polytrichum strictum was due to a combination of environmental and genetic factors.

The applicability of the results from this study to other areas where _Tomenthypnum_ _nitens_ and the Feather mosses occur, therefore, depends on the genetic variation in these species and the morphological and physiological plasticity which they are able to exhibit. The general climate of the area near Edson appears comparable to the climate of other areas where these species are conspicuous components of the vegetation (Tamm 1953, p.136; Ritchie 1960; Ruuhijärvi 1960; Heinselman 1963; Sjörs 1963). However it is not always possible to use climatic data to determine whether microclimates are comparable. In this case solar radiation and air temperature were comparable with data recorded at a nearby meteorological station at Edson, but parameters such as rainfall, moss temperature, evaporation and wind showed variation on a more local scale. In a region of variable topography, relationships between microclimate and macroclimate can be very poor (e.g. Billings and Anderson 1966) and this is a major problem in attempting to correlate species distributions with maps of meteorological factors (compare Forman 1964 with Dilks and Proctor 1975). The macro- and micro-climatic data presented in this study should, however, prove valuable for controlled environment studies of physiological responses and in comparing the growth rates and habitat limits of these species with other populations in different regions.

VI. CONCLUSIONS

The *Tomenthypnum nitens* community in the open fen is exposed to higher levels of solar radiation, higher canopy surface temperatures, greater surface temperature variation, and higher evaporation stress than the more sheltered Feather moss community. The Feather mosses receive less rainfall because of interception by the tree canopy and are subjected to frequent drought stress because, unlike the *T. nitens* community, they occur in well-drained habitats with no access to ground water.

Growth rate of *T. nitens* depends on water content of the apical region which, in turn, is determined by the balance between movement of water from the water table up through the canopy and loss through evaporation. The canopy morphology is well adapted for this process; the closely packed stems reduce evaporation within the canopy and the stem tomentum and stem leaves provide a low-resistance path for water movement. Rate of water movement through the canopy is probably controlled by depth to the water table, and this water level, at least in part, may be controlled by the total annual precipitation - evaporation balance. Long-term growth of the *T. nitens* canopy is probably determined by changes in ground-water level and decomposition rate. Growth of *T. nitens* in less hydric habitats appears to be inhibited by restricted access to ground water and this water requirement does not appear to be satisfied by precipitation, even in habitats with a lower evaporation stress.

Growth rate of the Feather mosses appears to depend on the length of time which the mosses are wet, which is determined by the frequency of precipitation. Feather mosses may have a higher net assimilation rate and may be more drought tolerant than T. nitens which could explain their dominance in less hydric habitats; however their establishment and growth in the fen appears to be limited by susceptibility to radiation damage and by deleterious effects of saturation by water supplied from the groundwater table. Survival of these species outside a tree canopy is possible if they are protected from evaporation stress, but growth and survival depend on the maintenance of a high apical water content for substantial periods after rain and this requires at least some protection from solar radiation and wind.

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APPENDIX I

Species Composition of Study Site Plant Communities

In the following table A to M refer to the plant communities discussed in the text and the numbers associated with the species names are their cover-abundance values (Braun-Blanquet 1964), on a scale of + to 5, in each community. Unless otherwise indicated, nomenclature for vascular plants follows Moss (1959), that for mosses follows Crum et al. (1973), and for lichens Hale and Culberson (1970).

Species	A	B	C	D	E	F	G	H	J	K	L	M
TREES												
Larix laricina		2	2	+	1							
Populus balsamifera								+			+	
Pinus contorta var. *latifolia*					+			2	+	2	2	1
Populus tremuloides								+	+	2	1	3
Picea mariana		+	1	2	4	5	5	2	+	2	+	+
Picea glauca												+
SHRUBS												
Andromeda polifolia	1		1	+								
Salix bebbiana					+							
Betula pumila var. *glandulifera*	+	3	3	+	1							
Salix candida		+	+	+	1							
Oxycoccus microcarpus		+	+	+	+	+						
Salix maccalliana			+			+						
Salix myrtillifolia					+	+						
Rubus chamaemorus						+	+					
Lonicera involucrata					+	+	+	+				

Species	A	B	C	D	E	F	G	H	J	K	L	M
Ribes hudsonianum					+	+				+		
Alnus crispa					+					3	+	3
Ledum groenlandicum				1	1	3	+	2	+	3	+	+
Vaccinium vitis-idaea var. *minus*				1	+	+	+	1	1	+	2	+
Linnaea borealis var. *americana*					+	+		+	+	+	+	+
Rosa acicularis					+	+		+	+	+	+	+
Vaccinium myrtilloides					+	+	+	+	+	+	+	+
Arctostaphylos uva-ursi								+	2	+	3	+
Shepherdia canadensis										+	+	
Rubus strigosus												+
Viburnum edule												+
HERBS												
Drosera anglica	+											
Juncus albescens	+											
Utricularia intermedia	1											
Muhlenbergia glomerata		1										
Parnassia palustris var. *neogaea*		+										
Lobelia kalmii	+	+										
Carex atherodes		+										
Carex limosa			1									
Carex vaginata			+									
Carex lasiocarpa	+		+									
Tofieldia glutinosa	+		1									
Triglochin maritima	+		+									
Carex diandra	+	1	+									
Carex interior	+	1	1									
Habenaria hyperborea	+	+	1									
Calamagrostis inexpansa				1								

Species	A	B	C	D	E	F	G	H	J	K	L	M
Eriophorum scheuchzeri	+	+	+	+								
Menyanthes trifoliata	1	1	2	+								
Spiranthes romanzoffiana	+	+	+	+	+							
Campanula rotundifolia		+	+	+		+						+
Caltha palustris			+		+							
Pedicularis labradorica			+		+							
Potentilla palustris			+	+								
Orchis rotundifolia			+	+	+							
Carex aquatilis			1	+	1	+						
Ranunculus lapponicus						1						
Smilacina trifolia			1	+	+	+	+					
Equisetum fluviatile	+		1	+	+		1			+		
Carex disperma				+	+	+	+					
Equisetum scirpoides				+	+	+	+	+				+
Petasites palmatus					+	+	+	+				
Equisetum sylvaticum						1		+				
Equisetum pratense					1		2	+	+	+		
Epilobium angustifolium					+	+		+	+	+	+	+
Cornus canadensis					+	1	+	+	+	+		+
Geocaulon lividum						+	+	+	1	+	+	+
Equisetum arvense						+	+				+	+
Lycopodium complanatum								1				+
Antennaria neglecta									+			
Galium boreale									+	+	+	+
Maianthemum canadense var. *interius*									+	+	+	+
Pyrola secunda									+	+	+	+
Anemone multifida									+		+	+
Viola renifolia										+		

Species	A	B	C	D	E	F	G	H	J	K	L	M
Solidago decumbens var. *oreophila*											+	
Pyrola virens											+	
Aralia nudicaulis												2
Aster ciliolatus												+
Aster laevis var. *geyeri*												+
Goodyera repens												+
Lycopodium annotinum												+
Pyrola asarifolia												+
CRYPTOGAMS												
Calliergon trifarium	1											
Drepanocladus revolvens	2											
Meesia triquetra	1											
Scorpidium turgescens	2											
Campylium stellatum	+	+										
Cladonia cornuta		+										
Sphagnum angustifolium (Russ.) C.Jens.			+									
Cladina rangiferina				2								
Stereocaulon tomentosum				+								
Bryum pseudotriquetrum		+	+	+								
Sphagnum warnstorfii			1	+								
Sphagnum fuscum			1									
Tomenthypnum nitens	+	5	5	+	1	+						
Dicranum undulatum		+	+	+	+		+					
Aulacomnium palustre		+	+	2	+	+	+					
Sphagnum nemoreum Scop.					+	1						
Plagiomnium ellipticum (Brid.) Kop.					+	+	+					
Cladina mitis				2		+		1				

Species	A	B	C	D	E	F	G	H	J	K	L	M
Dicranum polysetum				+	+	+			+	+		
Ptilium crista-castrensis				+	+	2	2	2				
Peltigera apthosa				+	+	+	+	+	+	+		+
Hylocomium splendens				+	+	2	3	3	+	2	+	+
Pleurozium schreberi				+	+	3	3	2	+	3	+	+
Polytrichum strictum						+		+			+	
Peltigera malacea								+	+		+	
Ceratodon purpureus									+		+	
Cladina arbuscula											+	

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THE UNIVERSITY OF ALBERTA

ENERGY AND WATER RELATIONS OF SOME BOREAL FOREST MOSSES

by

© JOHN ROBERT BUSBY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Energy and Water Relations of some Boreal Forest Mosses submitted by John Robert Busby in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Ecology

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To my parents.

They set the example...

ABSTRACT

Tomenthypnum nitens (Hedw.) Loeske forms dense carpets in fens where the tree and shrub canopy is sparse and the water table is close to the surface. The Feather moss species [*Hylocomium splendens* (Hedw.) BSG, *Pleurozium schreberi* (Brid.) Mitt., and *Ptilium crista-castrensis* (Hedw.) De Not.] form more open carpets in shaded and better drained habitats. A study was made of the environments of these moss communities at a site near Edson, Alberta and parameters controlling growth rates and habitat limits of the species were investigated.

Global short-wave radiation incident on the Feather mosses under a tree canopy averaged 20% of that on *T. nitens* in the open. Diurnal air temperature fluctuations were about 4.5°C lower under the forest canopy than in the open. The canopy surface of *T. nitens* showed large temperature variation, with temperature elevations as high as 15°C above ambient air, while the Feather mosses, except when exposed to sun-flecks, had surface temperatures close to air temperature. Free surface evaporation rate over forested Feather moss sites averaged 57% of that in the open over *T. nitens*, while rainfall reaching the Feather mosses averaged 78% of that reaching *T. nitens*. Mean wind speeds over the Feather mosses were also lower than over *T. nitens*.

Measurements showed that the capacity for net assimilation decreased with depth from the canopy surface in

all species, and that net assimilation rates decreased with decreasing water contents below 3 g • g dry wt^{-1}, and approached zero at water contents below 0.4 g • g dry wt^{-1}. Optimal light levels for H. splendens and T. nitens were found to be 250 and 150 µ Einstein m^{-2} sec^{-1} respectively. In addition, the relationships between water content and water potential were determined for all species.

Growth of T. nitens was measured relative to small wire stakes and net production from May to October 1975 averaged 190 g m^{-2}. Spatial variation in growth rate was correlated with the colour of the apical region and appeared to be caused by variation in apical water contents. Seasonal variation in growth rate was correlated with depth from the canopy surface to the ground water table. The growth rate of T. nitens was probably controlled by the balance between rate of transport of water through the canopy and loss through evaporation. The most important environmental factors appeared to be total precipitation, followed by evaporation stress.

Growth of the Feather mosses was estimated by measuring dry weight changes of layers of Hylocomium splendens, and net production from May to October averaged 79 g m^{-2}. Growth was correlated with the length of time that the moss was wet and thus was probably controlled by frequency of precipitation. Since growth rates were measurably reduced by removal of a sparse shrub canopy, evaporation stress was probably a second important factor.

Survival and growth of Tomenthypnum nitens appeared to be limited by evaporation stress in habitats where ground water was not available. Feather mosses appeared to be limited by radiation damage and evaporation stress in open habitats, by depression of net assimilation and other deleterious effects of saturation in wet habitats, and by insufficient rainfall under dense tree canopies.

ACKNOWLEDGEMENTS

I would like to thank Dr. L.C. Bliss, my supervisor, for his guidance of my Ph.D. program and unqualified support, both academic and financial, during the evolution and execution of this research. Special thanks also go to Dr. D.W.A. Whitfield for assistance in designing the micromet measuring procedures and net assimilation measurements, to Dr. J.M. Mayo for valuable pointers on the net assimilation measurements and methods of investigating the water relations of the species, and to Dr. D.H. Vitt for assistance in selecting the species and the field site. I would also like to thank these, and the other members of my examining committee, for their conscientious review of this thesis.

My greatest appreciation, however, is reserved for Cathy, my wife, who assisted me with the field work, prepared all the plates and most of the figures, and reviewed and criticised the numerous drafts of this thesis.

Ms. M. Dumais verified all the vascular plant specimens, Dr. Vitt verified the bryophytes, and Marianne See and Mike Ostafichuk verified the lichens. Various of my fellow graduate students, including Paul Addison, Tom Lee, John Harter and Al Black, helped out with various phases of the field work and provided more or less willing audiences for some of my ideas.

This course of study was undertaken while I was in receipt of a Canadian Commonwealth Scholarship, and the

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I. INTRODUCTION

Mosses occupy a significant proportion of the land area and form a conspicuous component of the vegetation throughout boreal regions in North America, Europe and Asia. Little is known, however, about the environmental factors which control their growth rates and habitat limits, or even what the environmental characteristics of these habitats are.

Mosses not only have considerable ecological importance in the boreal forest, but their tendency to grow in uniform carpets of one or a few species facilitates investigations of the role of microclimatic factors in controlling the growth and distribution of plant communities. The more or less even canopy surfaces, the relatively small air spaces between the stems, and the general absence of any significant below ground growth make them ideal subjects for detailed study of environment-plant community interactions. Progress in this area should be rapid once the basic controlling factors have been established.

Water appears to be a major factor in controlling growth and distribution of mosses. Their water relations, however, are fundamentally different from most higher plants. They lack root systems, conducting systems are generally not as well developed as those of vascular plants, and they have no mechanisms for water storage or, as individuals, to reduce water loss. Anderson (1974) recently stated that:

> "The water regime to which nearly all non-aquatic bryophytes are adapted is as follows: saturation of plants by rain, dew or fog; immediate increase in metabolic activities, including resumption of photosynthesis within minutes, if or as soon as there is sufficient light; when rain stops and humidity drops, plants begin to lose water by evaporation; as plants dry out, metabolism, including photosynthesis, decreases, and at a certain level of desiccation photosynthesis stops, other metabolic activities decline to a low level commensurate with temperature, and growth slows and eventually ceases; plants remain inactive until rewetted, when the routine begins anew."

While this description applies to dry habitat species which have little or no access to substrate water, the situation with mosses growing in wetter habitats is more complex. Discussion of the source of water for such species and of the importance of the central conducting strand (when present) in its transport, in fact, has a history of controversy extending back to the 1880's (see Blaikley 1932). Most bryophyte species do not posess central conducting strands and water movement is primarily via external capillary spaces between the leaves and along the stems (Bowen 1931, Mägdefrau 1935, Anderson and Bordeau 1955, Tallis 1959). In most species, however, the relative importance of water from the atmosphere (rain, snow, fog, dew, etc.) or from the substrate, and the effects of other environmental factors in regulating rate of gain or loss of water have not been studied.

Rates of loss and frequency of wetting and drying can be critical in controlling moss growth and distribution.

Rate of water loss from individual stems is comparable to that from a free water surface (Barkman 1958, p.81), and bryophytes inevitably lose water, except in a saturated atmosphere (Tennant 1953; Tallis 1959, 1964; Hinshiri and Proctor 1971). Rate of water loss, however, can be greatly modified by the morphology of the moss canopy, i.e. the growth form of the moss (Tallis 1959, Hosokawa *et al*. 1964). A close correlation between growth form and habitat has been frequently noted (Gimingham and Robertson 1950, Hamilton 1953, Seim *et al*. 1955), and some studies have attempted to identify some of the parameters involved (Gimingham and Birse 1957; Birse 1957, 1958a,b; Gimingham and Brynard 1959). Understanding of cause and effect relationships, however, requires the integration of laboratory physiological studies and field experimental work and very few studies of this type have been done (see, however, Forman 1964).

The growing region of the moss at the canopy surface is not protected from water loss and, since no water conserving structures are present, is subject to desiccation if the water supply is interrupted. Differences in apical morphology have a negligible effect on resistance to water loss and any resistance to desiccation stress is exhibited in the cytoplasm (Patterson 1964, Lee and Stewart 1971, Dilks and Proctor 1975). Differences in tolerance to and recovery from desiccation would therefore be expected to significantly influence the growth rates and habitat limits of the moss species.

Other environmental factors such as radiation, temperature, evaporation stress and wind are also important, along with factors such as carbon dioxide concentration, nutrient balance, grazing and species reproduction, dispersal and establishment (see Barkman 1958, p.171).

Solar radiation has a number of direct and indirect effects on mosses, providing not only energy for photosynthesis but also for evaporation of water from the canopies. High levels of radiation may also have a direct damaging effect on some species (Levitt 1972, p.451). Temperature influences rates of metabolic processes and evaporation rates and evaporation stress, precipitation, and wind also influence the species' water status.

This study was designed to investigate the effect of physical environmental parameters on the water relations, growth rates and relative distributions of two boreal forest moss communities. The influence of other parameters such as chemical (CO_2, nutrients) and biotic (grazing, reproduction, etc.) factors, though likely to be important in various aspects of the ecology of the species concerned, were considered beyond the scope of this project and were not investigated.

The study was confined to the snow-free season from May to October. This was due not only to logistic considerations but also the fact that, although mosses may be metabolically active during the winter (Tamm 1953, p.20;

Atanasiu 1969, 1971), evidence suggests that growth is negligible during this season in continental and polar regions (Tamm l.c.; Longton and Greene 1969; Longton 1970, 1972b) and that snow cover appears to have a negligible effect on moss distribution (Tamm 1953, p.105).

The objective was to select, and then to compare and contrast, moss communities from two different habitats. The criteria for selection were that the canopies had to be robust (depth of living or potentially living material greater than 5 cm), more or less homogeneous (either a single species or a few species with similar growth forms), and had to cover areas large enough so that there would be no shortage of material for sampling or manipulation experiments.

The communities selected were one consisting entirely of Tomenthypnum nitens (Hedw.) Loeske and another consisting of a mixture of Hylocomium splendens (Hedw.) BSG, Pleurozium schreberi (Brid.) Mitt., and Ptilium crista-castrensis (Hedw.) De Not. The last three species are collectively defined as 'Feather mosses'.

An additional feature of the species selected is that they are all circumboreal (Schofield 1969, Crum 1973) and are conspicuous components of vegetation types which occupy substantial areas in the boreal region. Results from this study should, therefore, with appropriate qualification, be applicable to many of the other areas where these species occur.

Tomenthypnum nitens (Plate 1a) is widely distributed in boreal and Arctic regions (Schofield 1972; Crum 1973, p.282; Vitt and Hamilton 1975). Details of the morphology can be found in Crum (1973, pp.281-282), but the salient features of interest in this study are that the stem and branch leaves are numerous and closely spaced and numerous rhizoids arise from the bases of the stem leaves forming a dense tomentum. This tomentum is more or less continuous from the apex to the base of the stems and tends to predominate on one side (Plate 1a, see also Vitt and Hamilton 1975). The species is rather robust and forms dense carpets in fens throughout its range (e.g. Katz 1926, Moss 1955, Sjörs 1961, Khodachek 1969, Holmen and Scotter 1971, Vitt and Hamilton 1975). Its habitat, which will be described more fully in subsequent sections, is usually characterized by a sparse tree and shrub component and a high water table. Its canopy can be classified into the growth form categories of "Tall turfs, divergent branches of limited growth" (Gimingham and Birse 1957) and "Tall turfs (rhizoidal)" (Birse 1958a). These authors note that mosses in these categories characteristically occupy habitats where they are always within reach of the water table.

The Feather moss community, with some variation in the proportions of the component species, is found throughout the boreal regions of Canada (Lewis *et al*. 1928, Moss 1955, Ritchie 1956, Sjörs 1961, Looman 1964, Jeglum 1973, Jeglum *et al*. 1974, LaRoi and Stringer 1976), northeastern United

Plate 1

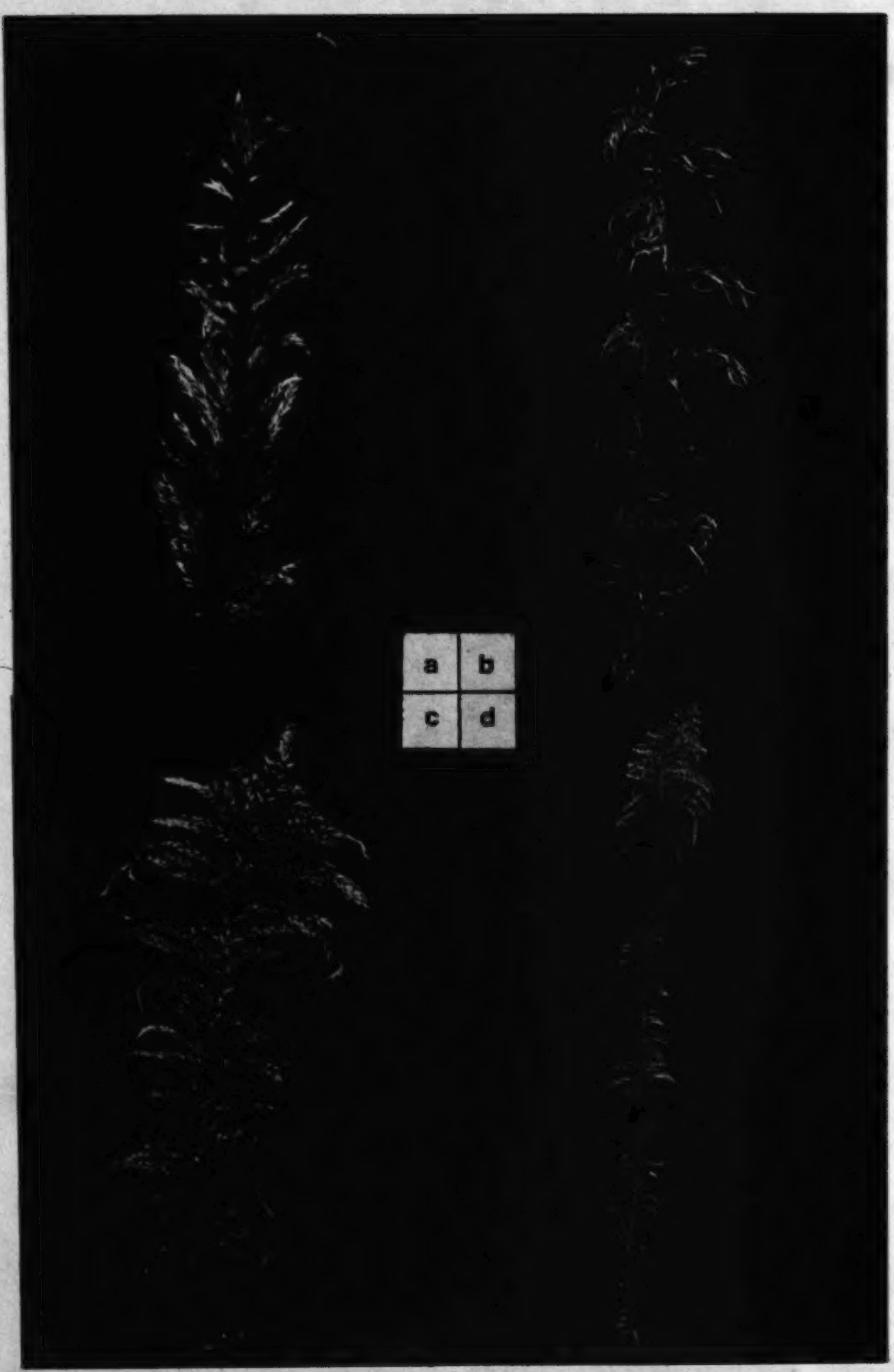
Morphology of Tomenthypnum nitens and the three Feather mosses:

a) Tomenthypnum nitens (Hedw.) Loeske (x 1.5)

b) Hylocomium splendens (Hedw.) BSG (x 1.3)

c) Pleurozium schreberi (Brid.) Mitt. (x 2)

d) Ptilium crista-castrensis (Hedw.) De Not. (x 1)


a
b
c
d

States (Seim _et_ _al_. 1955, Buell and Niering 1957, Heinselman 1963, Billings and Anderson 1966), Fenno-Scandia (Tamm 1953, Ruuhijärvi 1960) and the Soviet Union (Sukachev 1928, Abolin' 1974, Tarkhova and Ipatov 1975). The species are all included in the "Weft" growth form category, the characteristic features of which are "Shoots long, straggling, generally robust, rhizoids usually sparse, laterals often arched or ascending. A loose inter-twining of straggling shoots and branches" (Gimingham and Birse 1957). Moss with the weft growth form characteristically occupy shady and/or humid habitats (_ibid_.).

Hylocomium _splendens_ (Plate 1b) has a wide geographical distribution and occurs in a variety of habitats including alpine, subalpine, boreal and arctic vegetation (Billings and Drew 1938; Tamm 1953; Khodachek 1969; Holmen and Scotter 1971; Crum 1973). Crum (1973, pp.342-343) contains distributional data and a morphological description of the species, the features of interest in this study being "Stems stiff and wiry, regularly 2-3-pinnate in horizontal fronds in a step-wise arrangement, each frond produced by an arched and ascending, stoloniform innovation arising from the middle of the previous year's growth." This feature of annual growth increments was used by Tamm (1953) to examine the seasonal growth of this species and to relate growth to light and nutrient status.

Pleurozium _schreberi_ (Plate 1c) has a more restricted geographical range in North America than _H_. _splendens_ and mainly occurs in boreal and subarctic regions. It is, however, very widely distributed in Great Britain (Longton and Greene 1969) and predominates in the Feather moss communities in the Great Lakes region of North America (Seim et al. 1955, Buell and Niering 1957, LaRoi and Stringer 1976). A morphological description and distributional data can be found in Crum (1973, pp.302-304).

Ptilium crista-castrensis (Plate 1d) appears to have a more restricted geographical distribution than the other Feather mosses and, although a consistent member of the Feather moss community, rarely seems to be prominent. A description of its morphology and distributional data can be found in Crum (1973, pp.334-335).

The three Feather mosses are roughly similar in size and growth rate and their growth forms are comparable enough for the Feather moss canopy to meet the selection criteria of relative homogeneity. Attention will be focussed primarily on Hylocomium splendens because the annual growth layer phenomenon facilitates comparison between growth rates and environmental factors, but the other species will be included where appropriate.

There were three main objectives in this study. The first was to make a detailed description of the habitat and microclimate of the moss communities studied, in order to provide information which would be useful in establishing controlled environments for further detailed physiological work and to provide baseline data for comparison of moss communities in western Alberta with similar communities elsewhere in the boreal region. The second objective was to measure the growth rates of the species during the snow-free season and to correlate growth rates with environmental factors in an attempt to identify the parameters controlling the growth rates. The third objective was to investigate the factors which might control the habitat limits of the species and to determine how these factors operate.

II. STUDY AREA AND ENVIRONMENT

1. Location of Study Area

The field study site is located in west-central Alberta at 116°36'W 53°29'N, the full legal description being the northern half of Legal Subdivision (LSD) 5 and the southern half of LSD 12, Section 16, Township 52, Range 18, West 5th Meridian (Fig. 1).

The site is a small mire which has developed at the head of a catchment and which is bordered by forest on the north, west and south sides. The mire drains to the east, via another mire, into the McLeod River (Fig. 1). Access to the area is by a road along a ridge on the north side.

The study area is delimited to the north, west and south by the catchment boundaries, and to the east by the boundary between LSD's 5 and 12 and LSD's 6 and 11 (Fig. 2).

2. Vegetation

The vegetation of the mire and its catchment was subdivided into community types on the basis of vegetation structure and floristic composition. Within the 7.1 ha region 12 community types were subjectively distinguished, and a list of the common species with their cover-abundance values (Braun-Blanquet 1964) was made for each (Appendix I). Voucher specimens were collected and are deposited in the

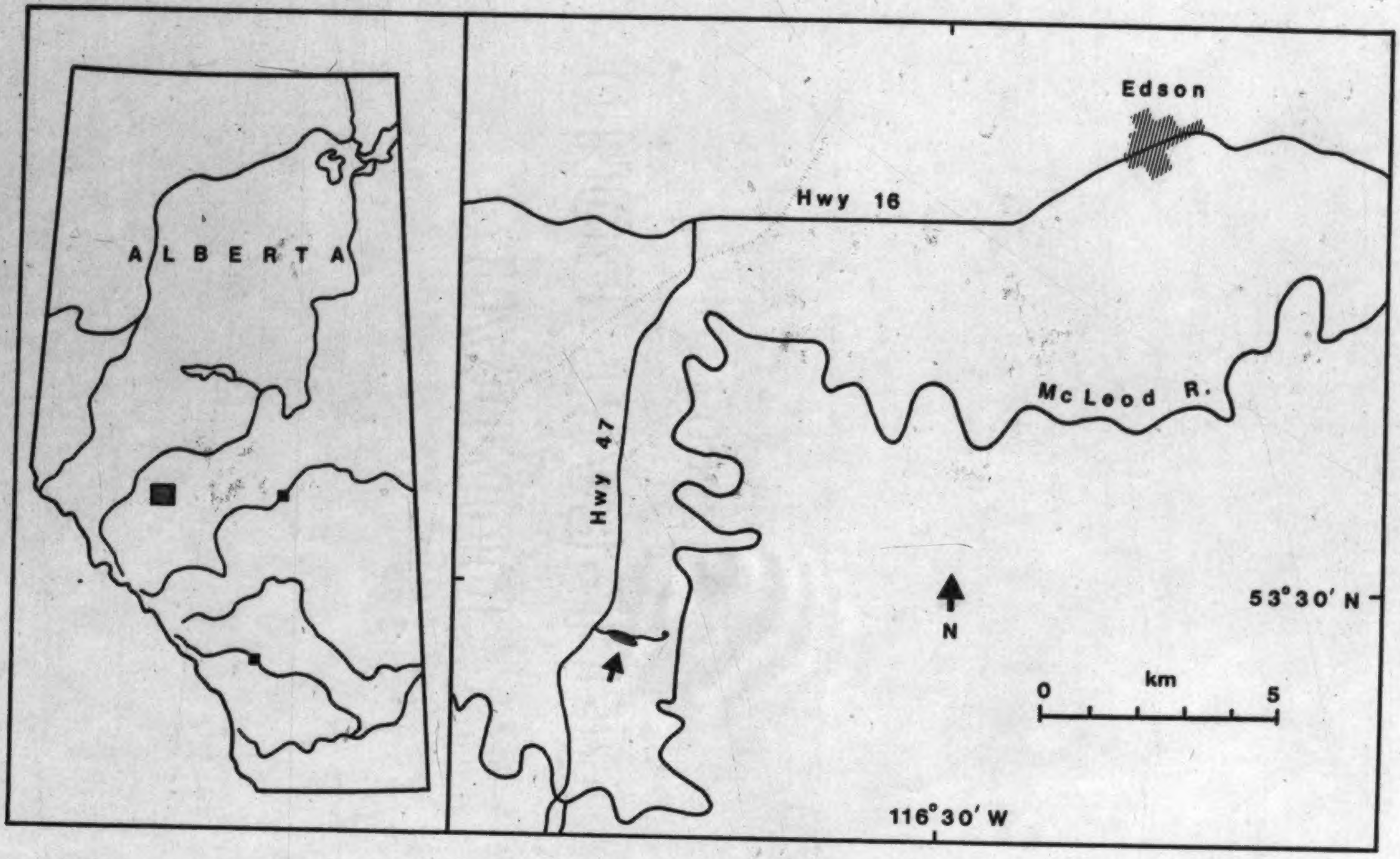
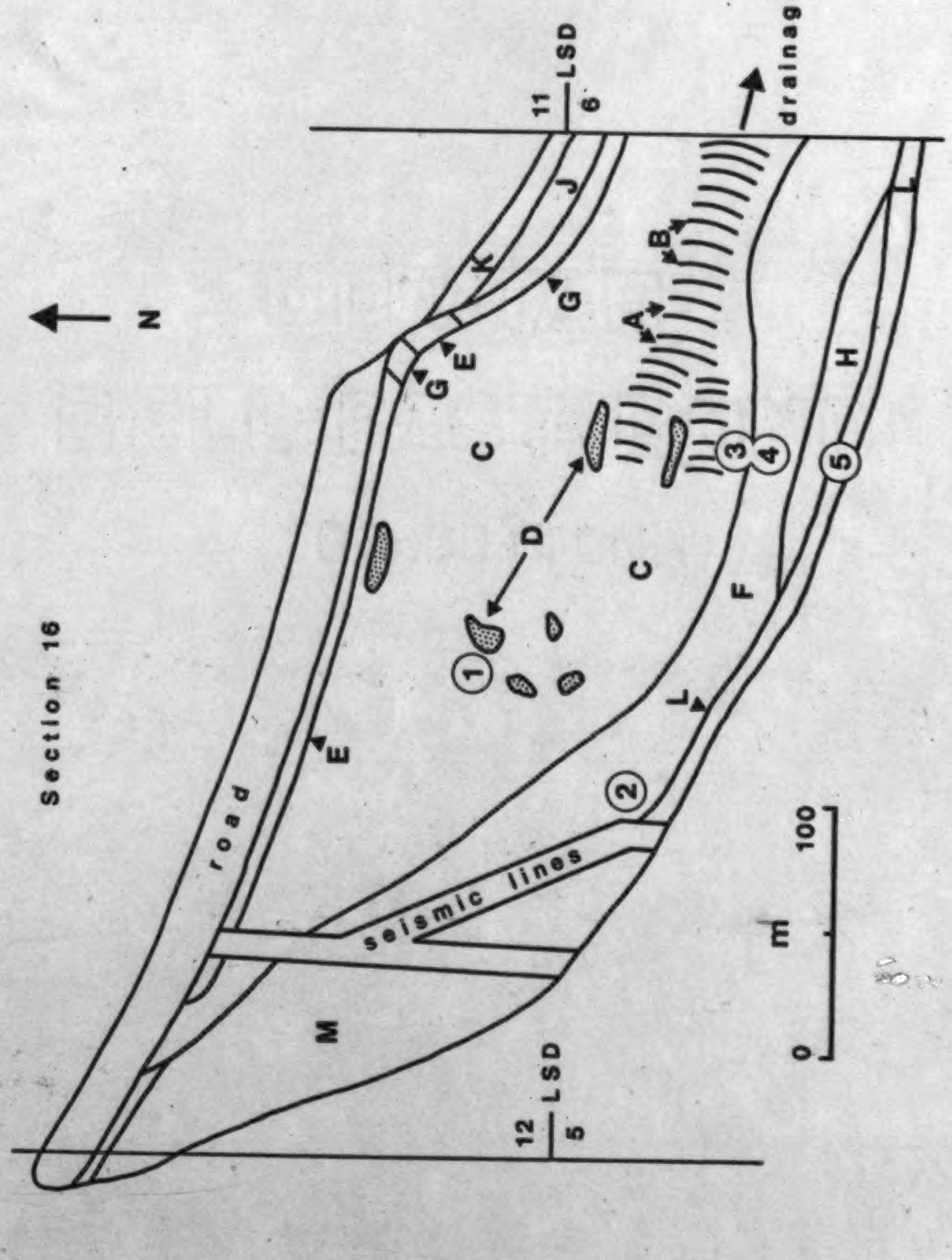

ALBERTA
Edson
Hwy 16
Hwy 47
Mc Leod R.
N
53°30′ N
116°30′ W
0
km
5

Figure 1. Location of study site 15 km s.w. of Edson, in west-central Alberta, Canada.

Figure 2

Site vegetation and location of experimental sites. The letters A-M refer to vegetation types (see text).

1 = *Tomenthypnum* meteorological site
2 = Feather moss meteorological site
3 = *Tomenthypnum* transplant site
4 = Feather moss transplant site
5 = Ridge-crest transplant site


Section 16
N
road
seismic lines
M
12
5
LSD
11
6
LSD
drainage
C
C
D
E
E
G
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K
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The mire itself (veg. type C in Fig. 2 and Appendix I) occupies about 3.4 ha and consists of scattered trees with an understory of shrubs and herbs and an almost complete bryophyte cover (Plate 2a). The tree crown cover was estimated to be about 10%, consisting entirely of *Larix laricina*[1] (height 2 to 6 m) and *Picea mariana* (2 to 5 m). Taller specimens of *P. mariana* (up to 12 m) occur on small islands of elevated ground in the fen, the largest of which are shown in Fig. 2. The shrub layer is dominated by *Betula pumila* var. *glandulifera*, with a cover of about 20%, the herb layer by *Menyanthes trifoliata* and various species of *Carex*, and the bryophyte layer by *Tomenthypnum nitens*.

An area of about 0.36 ha in the south-eastern region of the mire shows a distinct patterning (Fig. 2). The pattern consists of parallel ridges and depressions oriented in a north-south direction, perpendicular to the direction of water movement. The ridges, or "strings" (veg. type B), are 1 to 2 m wide and support small *Larix laricina* (1 to 3 m) and occasional *Picea mariana* (0.5 to 1 m), an understory which includes *Betula pumila* var. *glandulifera*, and a complete ground cover of *Tomenthypnum nitens* (cf. Lewis *et al*. 1928).

The depressions, or "flarks" (veg. type A), are 2 to 3 m wide and contain standing water throughout the summer.

---

[1] Unless otherwise indicated, nomenclature for vascular plants follows Moss (1959), that for mosses follows Crum *et al*. (1973), and for lichens, Hale and Culberson (1970).

Plate 2

Study area and meteorological sites:

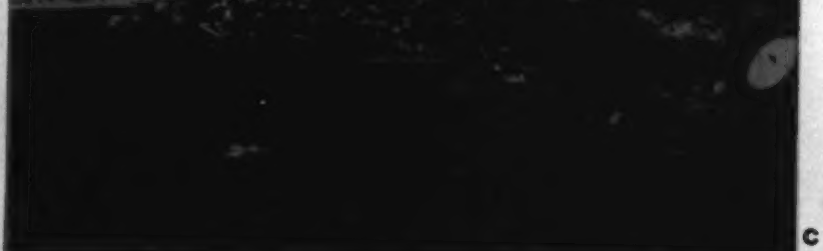
a) Fen vegetation in study area. Trees are *Picea mariana* (foreground) and *Larix laricina*, shrubs are *Betula pumila* var. *glandulifera*.

b) *Tomenthypnum* meteorological site. Recording rain gauge left foreground, evaporation gauge right foreground, anemometers centre, actinograph and hygrothermograph (in shelter) background.

c) Feather moss meteorological site. Trees are *Picea mariana*, shrubs are mostly *Lonicera involucrata*. Hygrothermograph (in shelter) left foreground, rain gauges and anemometer left centre, actinograph centre, soil temperature recorder right foreground.

a

b



c

The vegetation includes *Carex* spp., *Menyanthes trifoliata*, *Utricularia intermedia*, *Drosera anglica*, *Drepanocladus revolvens* and *Scorpidium turgescens*.

This mire complex can be considered a "rich fen" (Sjörs 1961), a "graminoid-rich treed fen" (Jeglum *et al*. 1974), or a "transitional wooded mire" (H. Trass, pers. comm. 1975), and will be subsequently referred to as a fen. Similar vegetation in Canada has been reported for Alberta by Moss (1955), the Northwest Territories, near the Alberta border, by Talbot (1975, cited in Vitt and Hamilton 1975), Northern Ontario (Sjörs 1961), and the west shore of Hudson Bay by Ritchie (1960), Sjörs (1963) and Ahti and Hepburn (1967). The vegetation resembles the "*Sphagnum warnstorfianum* - Braunmoore" described by Ruuhijärvi (1960) as part of the Aapamire complex of central and northern Finland (see also Moore and Bellamy 1974, pp.25-27). It also appears to correspond to the "Bryaleti" and "Cariceto-bryaleti" sub-types of the "Bryalo-parvocaricioni" peat types described by Tolpa *et al*. (1967, cited in Moore and Bellamy 1974, p.65) in the central European lowlands and a component of "Niedermoor" in central Russia (Katz 1926).

Patterns of strings and flarks, on various scales, are characteristic of this fen type (Heinselman 1963, Sjörs 1963), and the vegetation of the strings and flarks at the study site is very similar to that described for northern Ontario by Sjörs (*l.c.*).

An additional feature of this fen type is the scattered occurrence of *Picea mariana* islands. The mechanisms controlling the origin, development, and maintenance of these islands are not known (Heinselman 1963, Sjörs 1963). At the study site the islands (veg. type D) support a mixture of fen and forest vegetation under the *P. mariana* canopy. Species such as *Ledum groenlandicum*, *Vaccinium vitis-idaea* var. *minus*, *Cladina rangiferina*, *Cladina mitis*, *Hylocomium splendens* and *Pleurozium schreberi* occur on the more elevated regions, with *Aulacomnium palustre* and various other fen species occurring on the slopes. *Sphagnum warnstorfii* predominates on the north sides between the islands and the fen.

On the south side of the fen there is a transition zone dominated by *Sphagnum warnstorfii*, *S. angustifolium* (Russ.) C. Jens. and *S. fuscum* grading into a *Picea mariana* - Feather moss forest (cf. Lewis *et al*. 1928, Fig. 2). The *Sphagnum* zone varies in width from 3 to 4 m in the southeast of the fen to about 15 m in the southwest. The forest (veg. type F) occupies a more or less flat area of about 1.1 ha and consists of a tree canopy of *Picea mariana* (height 20 m, crown cover 80%), with an understory dominated by *Ledum groenlandicum*, *Equisetum sylvaticum*, *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*. Isolated stems of *Tomenthypnum nitens* occur in the wetter areas and small patches of *Aulacomnium palustre* are also present.

This forest type has a wide distribution across North

America (LaRoi and Stringer 1976) and can be clearly identified in vegetation studies from elsewhere in Alberta (Lewis *et al.* 1928, Moss 1955) and in Saskatchewan (Looman 1964, Jeglum 1973), Manitoba (Ritchie 1956), Ontario (Sjörs 1961, Jeglum *et al.* 1974), and Minnesota (Heinselman 1963). This vegetation also appears to correspond to the "Gemeine Bruchwalder" in Finland (Ruuhijärvi 1960), to the "Pineti" sub-type of the "Ledo-pinioni" peat type in central Europe (Tolpa *et al.* 1967, cited in Moore and Bellamy 1974, p.67), and to the *Piceeta hylocomiosa* in north and northwest Russia (Sukachev 1928).

On the north and northeast sides of the mire the fen species are replaced by forest species across a narrow zone at the base of the sand ridge which forms the northern boundary of the catchment. There is no well-developed *Sphagnum* zone but there is a greater predominance of *Larix laricina* and species of *Salix* compared with the fen's southern boundary. Part of this northern boundary forest (veg. type G) is very similar to the forest on the south side except that *Equisetum pratense* and *E. fluviatile* replace *E. sylvaticum*. The remaining northern boundary forest (veg. type F) is a mixture of fen and forest species. The tree canopy consists of *Picea mariana* along with *Larix laricina* and *Pinus contorta* var. *latifolia*. *Alnus crispa* and *Salix* species including *S. candida*, *S. myrtillifolia* and *S. bebbiana* form a conspicuous shrub layer, and the herb layer is very diverse, conspicuous species being *Equisetum* *pratense* and *Carex aquatilis*. The moss layer consists mainly of *Tomenthypnum nitens*, *Sphagnum nemoreum* Scop., and the three Feather moss species.

A road occupies the crest of the ridge on the north boundary of the study area, but the ridge delimiting the northeastern boundary has not been disturbed. The vegetation on this ridge (veg. type K) is well developed, with a tree canopy of *Picea mariana*, *Populus tremuloides*, and *Pinus contorta* var. *latifolia* having a total crown cover of about 50%. *Alnus crispa* (cover 60%) and *Shepherdia canadensis* are conspicuous in the shrub layer and the herb and moss layers are also well developed. *Pleurozium schreberi* and *Hylocomium splendens* have high cover values but *Ptilium crista-castrensis* was not recorded.

The vegetation on the south-facing slope of this ridge (veg. type J) is rather open with scattered individuals of *Pinus contorta* var. *latifolia*, *Picea mariana*, and *Populus tremuloides*. The understory vegetation has a rather xeric appearance with few tall shrubs and a herb and dwarf shrub cover consisting mainly of *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea* var. *minus*, and *Geocaulon lividum*. *Hylocomium splendens*, *Pleurozium schreberi*, and *Dicranum polysetum* are restricted to the lower part of the slope near the trees bordering the fen (veg. type G).

The north-facing slope of the ridge delimiting the southern catchment boundary has a more luxuriant plant community (veg. type H) than the south-facing slope described above. The tree species are the same, with the addition of *Populus balsamifera*, but have a higher cover, and the shrub layer of *Ledum groenlandicum*, and moss layer of *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* are very well-developed.

The crest of this southern boundary ridge supports a rather xeric plant community (veg. type L) which is similar to that of the south-facing slope (veg. type J) described above. The ridge crest vegetation, however, has a higher species richness and a better developed tree and shrub component.

The hill which forms the western boundary of the catchment supports a well-developed *Populus tremuloides* forest (veg. type M). Conspicuous species include *Alnus crispa* and *Aralia nudicaulis*; the over-all species richness is high.

3. Climate

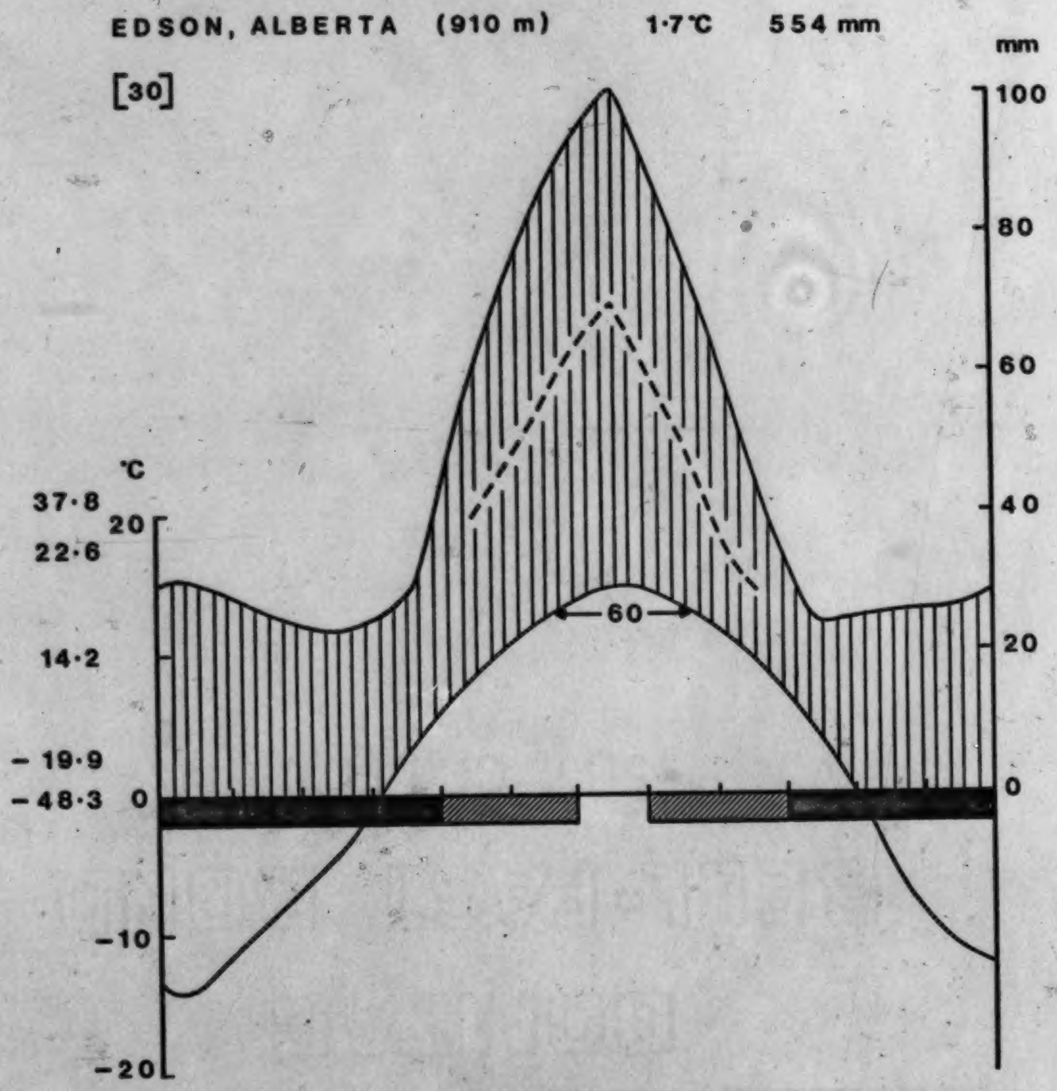
a) Macroclimate

The climate of the area can be described as Boreal Cold-temperate and meteorological data recorded by Environment Canada at Edson (see Fig. 1 for location) have been condensed into a climate diagram (Walter and Lieth 1960) (Fig. 3). The area experiences long, cold winters with moderate amounts of snow, and warm, humid summers with a frost-free season of about 60 days (The National Atlas of Canada 1974) and no substantial arid periods at any time.

This investigation was confined to the snow-free period from May through October, and various environmental parameters were measured during this time in 1974 and 1975.

b) Location of Meteorological Sites

Environmental measurements were made at sites which were representative of *Tomenthypnum* and Feather moss habitats. The *Tomenthypnum* site was located in an area free of, but more or less surrounded by, trees of *Picea mariana* and *Larix laricina*, and having a ground cover of *Tomenthypnum nitens* greater than 90% (Plate 2b and site 1, veg. type C, Fig. 2). The Feather moss site was situated under a dense canopy of *Picea mariana* near the middle of the north-facing slope of a sand ridge some 3 to 4 m in height (Plate 2c and site 2, veg. type F, Fig. 2). Combined cover



(Source: Environment Canada)

Figure 3.

Climate diagram for Edson, Alberta, after Walter and Lieth (1960). Mean annual temperature 1.7°C; total annual precipitation 554 mm; upper line is monthly precipitation; lower line is mean monthly temperature; frost-free days (minimum temperature > 0°C), 60; solid bar is months with mean minimum temperature < 0°C; diagonally hatched bar is months with absolute minimum temperature < 0°C. Temperatures on left (in ascending order); absolute minimum, mean minimum coldest month, mean diurnal temperature range, mean maximum warmest month, absolute maximum.

of the three Feather moss species was greater than 95%.

c) Methods and Results

Radiation

Global short-wave radiation was measured at the *Tomenthypnum* site with a Belfort bi-metallic actinograph from 5 June to 12 September 1974, and from 1 May to 1 November 1975. The objective was to measure seasonal trends in total daily short-wave radiation reaching a stand of *Tomenthypnum nitens*. Radiation was recorded continuously in units of cal cm^{-2} min^{-1}, the instrument being calibrated against a Kipp and Zonen Pyranometer which, in turn, had been calibrated in May 1975 by the National Atmospheric Radiation Centre, Ottawa.

Hourly readings of radiation were taken from the charts (the tracings being averaged by eye to obtain a mean value for each hour), multiplied by 60 to obtain total cal cm^{-2} for each hour, and summed over 24 hr to obtain the total daily radiation. These totals were averaged for five-day periods and are presented in Fig. 4.

The radiation totals are somewhat less than would be expected for a horizontal surface in the open because of radiation interception by trees surrounding the *Tomenthypnum* site, particularly in the early morning and late afternoon. This effect can be seen in the 0900 and 1800 hr values of

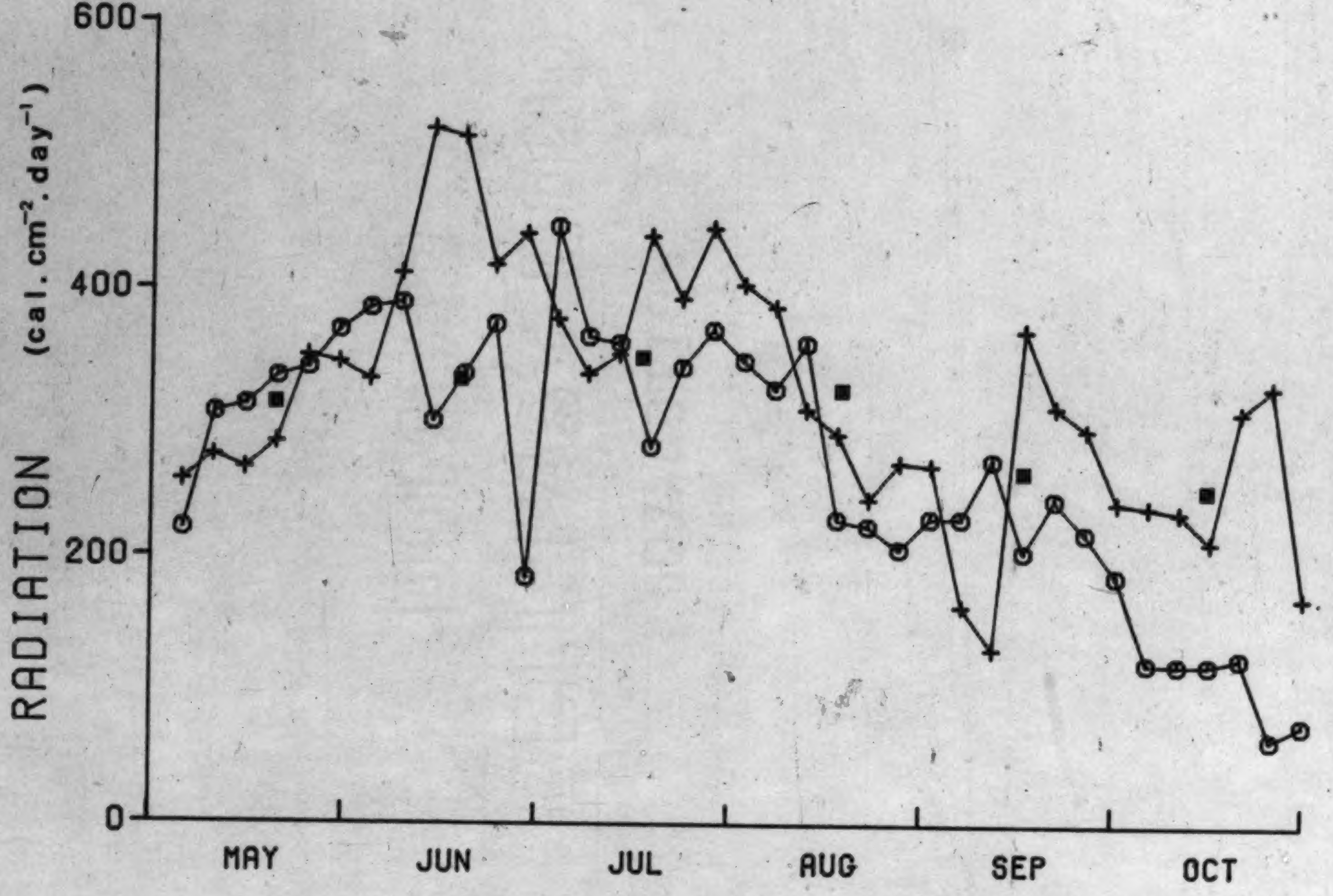


Figure 4. Five-day means of total daily global short-wave radiation at Tomenthypnum site: + = 1974; O = 1975; ■ = 30-year means.

the radiation curve for 15 to 24 June 1975 in Fig. 5.

The measurements for 1974, which did not extend over the whole season, were supplemented by data recorded by Environment Canada at Edson (Environment Canada 1974). Radiation is measured at this station by a Campbell-Stokes Sunshine Recorder which measures "units of bright sunshine", each unit being "sunshine intense enough to scorch or burn a standard card upon which the rays of the sun have been concentrated by a glass sphere" (Environment Canada 1974). The correlation coefficient between 94 daily radiation totals from the field site and the equivalent "bright sunshine" records from Edson was 0.86 ($p<0.001$). The sunshine records (X) were converted to cal cm^{-2} day^{-1} (Y) by the equation:

$$Y = 2.47\ X + 133$$

(which accounted for 73% of the variance). Converted sunshine data are a close approximation to the actinograph data, the average difference between equivalent readings being 11%. The converted Edson records were therefore used to supplement the 1974 data.

The data recorded by Environment Canada also included long-term monthly means for the years 1941 to 1970. These were also converted by the above equation and are shown in Fig. 4 which indicates the relationship of solar radiation in 1974 and 1975 to these long-term averages.

A major problem in using converted sunshine data is that the correlation between sunshine units and cal cm^{-2}

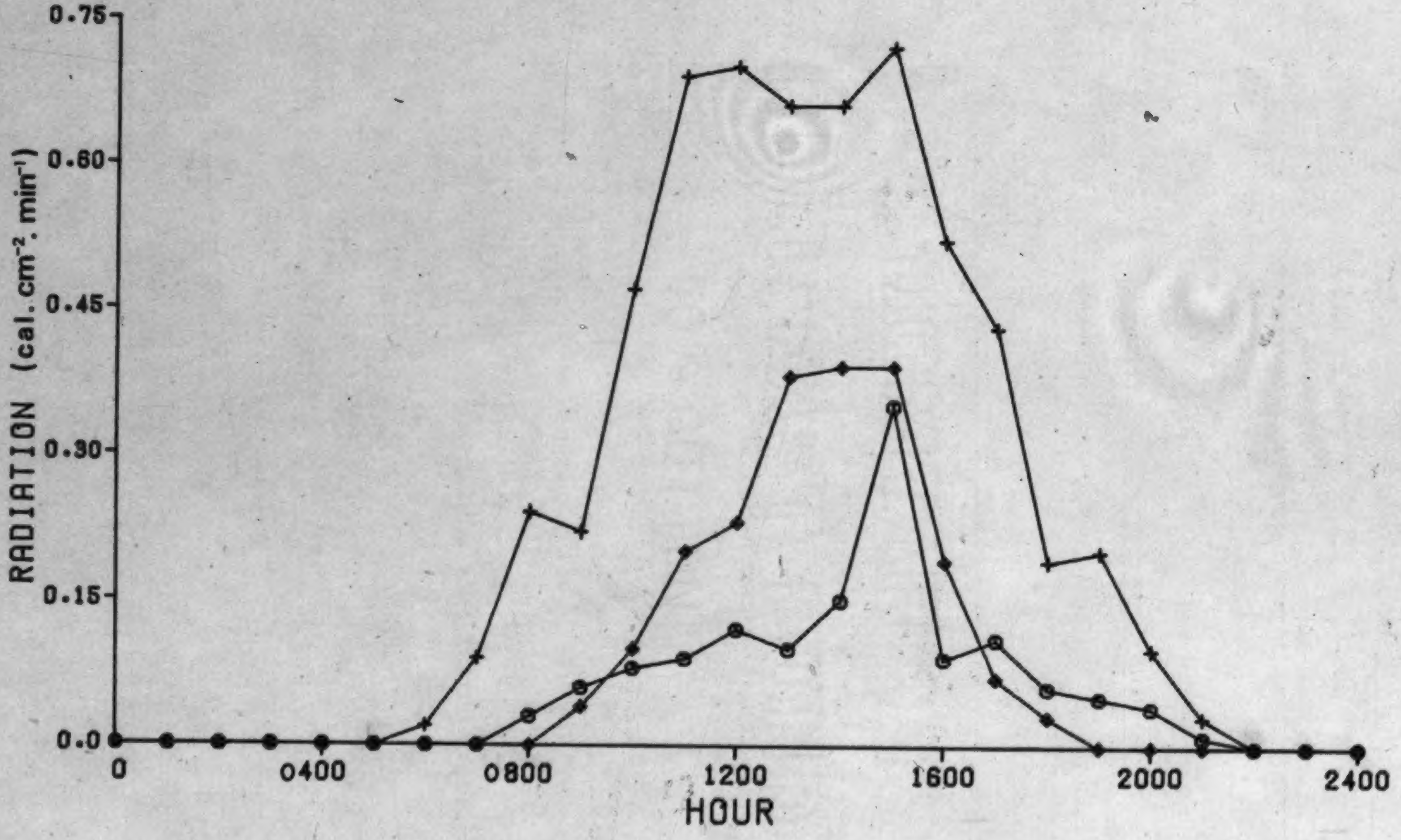


Figure 5. Mean hourly global short-wave radiation for ten day periods in 1975.
+ = *Tomenthypnum* site 15-24 June; ◆ = *Tomenthypnum* site 8-17 October;
O = Feather moss site 15-24 June.

day^{-1} decreases at low radiation levels to the point where a value of zero units cannot be converted since the cal cm^{-2} day^{-1} value could be anywhere between 0 and 133. This factor is obviously important on cloudy days, particularly late in the season. Other problems include the difference in cloud cover between Edson and the study area and interception of some of the radiation at the study site by surrounding trees, particularly late in the season when the sun angle is low. As a consequence of this last factor, the radiation estimates for September and October (both the long-term averages and the 1974 values) are probably a little high.

Similar radiation measurements were made at the Feather moss site. Comparison of 19 weeks of readings from 1974 and 16 weeks of readings from 1975 showed that the amount of short-wave radiation reaching the Feather moss carpet was 20±0.4% (mean±s.e.) of that recorded at the Tomenthypnum site. At six other Picea mariana - Feather moss stands in which radiation measurements were taken over seven day periods, the mean total radiation was 18% (range 17 to 21%) of the equivalent values at the Tomenthypnum site. These values compare with 14% reported for conifer-Feather moss forest by Buell and Niering (1957), and 4-40% reported for spruce forest by Geiger (1966, p.301). It is therefore apparent that the tree canopy intercepts more than 80% of the incoming short-wave radiation.

The Feather moss species, however, are not restricted to *P. mariana* stands. On the north side of the fen the three species occur in a more open habitat. Three weeks of radiation measurements in different locations in this habitat showed radiation totals of 34, 58 and 65% of those at the *Tomenthypnum* site for the same periods.

Diurnal patterns of radiation at the *Tomenthypnum* and Feather moss sites during different seasons were also examined. The greatest seasonal differences would be expected between mid-summer, when the sun angle is greatest, and the end of the season, when the sun angle is much lower. In order to obtain representative samples of each of these periods two ten-day intervals were chosen. Radiation totals for 15 to 24 June approximated long-term seasonal averages (Fig. 4), while the totals for 8 to 17 October, though probably below seasonal averages (difficult to determine due to the problems discussed previously), were at least representative of the month as a whole. Hourly radiation values for the *Tomenthypnum* site during each of the ten-day periods were averaged (Fig. 5). The apparent truncation of the June curve at mid-day is probably due to the presence of cloud. Field observations indicated that the period from dawn to 1000 or 1100 hr is generally clear, but cloud formation begins after this time and cloud build-up continues into the afternoon. The maximum radiation shown in Fig. 5 is 0.72 cal cm^{-2} min^{-1}, however values up to 1.25 cal cm^{-2} min^{-1} were recorded at around 1300 hr on cloudless days. The October curve reflects both the shorter day length and lower hourly radiation. The lower hourly radiation is a consequence of increased atmospheric scatter and increased interception by trees because of the lower sun angle. These factors all contribute to reduce the daily radiation totals of October compared with June.

Comparison of the Tomenthypnum site with the Feather moss site for the June period (Fig. 5) shows that the radiation level of the latter averages about 15% of that of the former, being about 0.1 cal cm^{-2} min^{-1}. However the sun shining through gaps in the tree canopy provides greatly increased radiation values, an example being the peak at 1500 hr in Fig. 5. These peaks may provide approximately 20% of the total daily radiation, a proportion which, of course, varies with location, cloud cover, and time of year. Feather moss mats receive, in October, approximately 20% of the radiation reaching the Tomenthypnum site, i.e. there does not appear to be any significant seasonal change in the relationship.

Up to this point the only radiation component discussed has been incoming short-wave radiation. Measurements were made in July 1974 to determine the relative contributions of various radiation components to the net radiation received by the moss canopy at both the Tomenthypnum and Feather moss sites. Downward short-wave radiation was measured with a temperature-shielded Kipp and Zonen Model CM-5 Pyranometer, and reflected short-wave radiation by a similar instrument inverted and mounted at a height of 1 m above the moss canopy. Both Pyranometers were calibrated in May 1975 by the National Atmospheric Radiation Centre, Ottawa. Long-wave down was calculated from measurements made with a Thornthwaite Net Radiometer mounted on a black-body cup surrounded by a water bath. The temperature of the bath was measured with a copper-constantan thermocouple connected to a cold junction compensator (Omega Engineering, Stamford, Conneticut). This temperature was then used to calculate radiation incident on the lower half of the radiometer by the expression:

$$\varepsilon \sigma T^4$$

where ε = emissivity (equals 1 for a black body),
σ = Stefan-Boltzman constant (8.13×10^{-11} cal cm^{-2} min^{-1} $^{o}K^{-4}$), and
T = water bath temperature (^{o}K).

Radiation on the upper half of the radiometer was calculated by adding the above value to the radiometer reading, and the long-wave radiation value was obtained by subtracting the short-wave component, as measured by the Pyranometer, from this sum. Long-wave up was calculated using the moss surface temperature, measured by averaging the readings of three fine (0.005 inch) copper-constantan thermocouples, and the expression:

$$\varepsilon \sigma T^4$$

where emissivity was assumed to be 0.975 (cf. Hoffman and Gates 1970) and T was the moss surface temperature (^{o}K). A Kahlsico Net Radiometer, mounted 1 m above the moss canopy, was used as a check on the radiation totals obtained by adding together the various components. The radiometers were calibrated against a Funk Net Radiometer also calibrated by the National Atmospheric Radiation Centre.

Radiation component values were collected at 0.5 hr intervals for a total of 12 days at each site, and the data condensed into 4 hr intervals to give a "typical" sunny July day at each site (Table 1). The first feature to note from this Table is that net radiation at the canopy surface is significantly lower than the incoming global short-wave radiation. This is due to the fact that some 14% of the incoming short-wave is reflected and that long-wave up exceeds long-wave down. The values in parentheses at 1300 hr in Table 1(a) represent the radiation components under cloudy conditions. Naturally, considerable variation would be expected, depending on cloud type and cover, but one feature of this example is that net radiation falls from 67% to 45% of the incoming short-wave radiation. In addition the energy input from long-wave radiation increases from 27% to 72% of the total input. It is apparent that information on all radiation components is necessary if further work on the role of net radiation in energy transfer processes is contemplated.

The values for short-wave down in Table 1(b) represent conditions in the shade. These values are, of course, greatly increased when the sun breaks through the tree canopy (cf. Fig. 5, p.29). The lower values for long-wave up at this site during daylight are explained by lower canopy temperatures which are a consequence of the lower

Table 1. Radiation components during a "typical" sunny July day. Values in parentheses represent cloudy conditions. All values are in cal cm^{-2} min^{-1}.

Hour	Short-wave Down	Short-wave Up	Long-wave Down	Long-wave Up	Net Radiation
		(a) *Tomenthypnum* site			
0100	0.00	0.00	0.46	0.49	-0.03
0500	0.00	0.00	0.44	0.46	-0.02
0900	0.95	0.13	0.44	0.60	0.66
1300	1.25 (0.20)	0.18 (0.03)	0.47 (0.52)	0.70 (0.60)	0.84 (0.09)
1700	0.86	0.12	0.50	0.62	0.62
2100	0.00	0.00	0.48	0.53	-0.05
		(b) Feather moss site			
0100	0.00	0.00	0.49	0.50	-0.01
0500	0.00	0.00	0.48	0.49	-0.01
0900	0.04	0.00	0.52	0.53	0.03
1300	0.07	0.01	0.55	0.57	0.04
1700	0.04	0.00	0.53	0.54	0.03
2100	0.00	0.00	0.51	0.51	0.00

incoming radiation.

An additional feature in Table 1 is the net radiation loss at night. The magnitude of this loss, however, is greater at the *Tomenthypnum* site than at the more sheltered

Feather moss site. Trees around the Feather moss site have a higher temperature, and therefore provide more long-wave energy, than the sky above the Tomenthypnum site (cf. Geiger 1966, p.305). The higher rate of energy loss of Tomenthypnum nitens means that its temperature may drop below that of the air, a feature which could be significant in dew formation (cf. Barkman 1958, p.70).

Air Temperature

Air temperature was recorded at the Tomenthypnum site, in the open, from 5 June to 12 September 1974, and from 1 May to 1 November 1975. The instrument, a Belfort Hygrothermograph, was calibrated at several different temperatures in a controlled environment chamber against a mercury thermometer. The hygrothermograph was placed in a white-painted, louvered shelter to protect it from solar radiation, and the shelter was placed on the moss canopy surface so that temperature could be monitored as close as practicable to the moss mat. Hourly temperature values were taken from the charts and used to calculate daily means. Daily mean temperatures, daily maximums and daily minimums were averaged over five-day periods and the values are presented in Fig. 6.

The measurements for 1974, which did not extend over the whole season, were supplemented by data recorded at standard height by Environment Canada at Edson (Environment

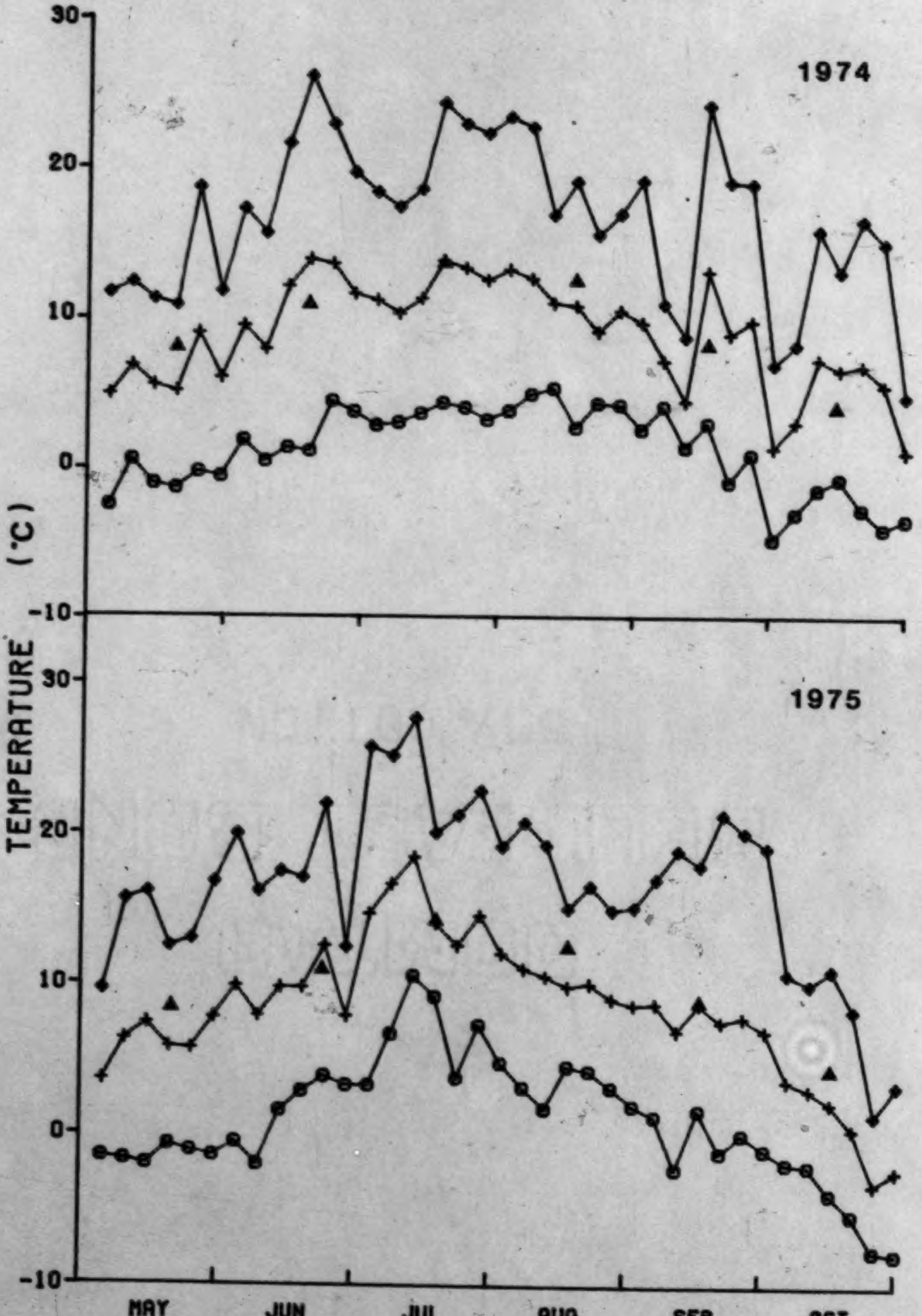


Figure 6. Five-day mean air temperatures at Tomenthypnum site: ◆ = maximum; + = mean; O = minimum, ▲ = 30-year means.

Canada 1974). The available information consisted of daily maximum and daily minimum temperatures, which were averaged to obtain the daily mean. The diurnal temperature variation, however, is not a regular sine curve so daily means based on maximum and minimum temperatures are not necessarily identical to those based on hourly readings. In order to supplement the field data by data recorded at Edson, it was necessary to establish the relationship between mean temperatures at the two locations. Comparison of 20 pairs of five-day means showed that the Edson means (X) were related to the *Tomenthypnum* means (Y) by the equation:

$$Y = 0.856\ X + 0.7$$

which accounted for 97% of the variance. There was a close correspondence between mean temperatures from the field site and the values from Edson which had been converted by this equation, the average difference between corresponding pairs of values being 0.3°C. Mean temperatures from Edson were therefore converted by this equation and used to supplement the 1974 field data in Fig. 6.

A problem with using the Edson records to extend the mean minimum temperatures at the field site was that minimum temperatures at the *Tomenthypnum* site were frequently lower than those recorded at Edson, sometimes by several degrees. This indicates that the *Tomenthypnum* site is a cold-air sink (cf. Nørgaard 1951, see also Geiger 1966, p.393). Comparison of 92 pairs of daily minimum temperatures for the field site and Edson showed a correlation coefficient of only 0.78, with the average temperature difference being 2.3°C. In many cases the temperature differences were very small, presumably on cloudy and/or windy nights. On the other hand differences as large as 7°C were noted. Differences in minimum temperatures, which presumably occurred most commonly on clear, still nights, were more pronounced on warmer nights. For example if the minimum temperature at Edson was between 8 and 10°C, then the minimum temperature at the field site was commonly as much as 5.5°C lower, whereas if the minimum temperature at Edson was between 0 and 2°C, then the minimum temperature at the field site was rarely more than 2.5°C lower. The relationship between daily minimum temperatures from Edson (X) and the Tomenthypnum site (Y) was found to be:

$$Y = 0.81\ X - 0.9.$$

This equation accounted for only 61% of the variance due to the variable degree of cold air drainage. The equation represents an "average" value for this phenomenon but it seems reasonable that it would provide a close approximation over five-day periods. It was therefore used to convert the Edson minimum temperatures which were then used to supplement the 1974 field data.

On the other hand comparison of the 92 pairs of daily maximum temperatures for the field site and Edson showed a correlation coefficient of 0.97, the average difference between equivalent pairs of readings being only 0.8°C. This indicates that the instrument shelter was effective in screening the hygrothermograph from radiation. The relationship between daily maximum temperatures from Edson (X) and the Tomenthypnum site (Y) was found to be:

$$Y = 1.04\ X - 0.7$$

which accounted for 94% of the variance. Maximum temperatures from Edson were therefore converted by this equation and used to supplement the 1974 field data.

The relationship between mean temperatures at Edson and those at the field site (i.e. $Y = 0.856\ X + 0.7$) was also used to estimate long-term monthly means (Table 2). These estimated long-term means are also shown in Fig. 6. Comparison of estimated with actual values for 1974 and 1975 shows a close agreement over the period from June to August. Further work, however, would be necessary to improve the agreement with other months, and it seems likely that the estimated long-term values for the field site in May, September and October may be about 1°C high.

Temperature data were recorded at the Feather moss site by another Belfort Hygrothermograph (calibrated against the first) from 3 June to 15 September 1974 and from 1 May to 3 August 1975. Comparison of 40 pairs of five-day means showed an average difference of 0.4°C between individual pairs of readings, with the Tomenthypnum site averaging an overall 0.16°C higher, so mean temperatures at the two sites were very similar. Diurnal temperature variations, however, were much greater at the open Tomenthypnum site than at the

Table 2. Mean monthly temperatures and long-term averages at *Tomenthypnum* site (°C).

	May	June	July	Aug	Sept	Oct
Edson Long-term Mean (1941-1970)	8.6	12.3	14.9	13.5	9.1	3.8
Study Site - Predicted Long-term Mean	8.1	11.2	13.5	12.3	8.5	3.8
1974						
Edson	6.6	12.8	13.4	12.0	8.3	5.4
Study Site - Predicted	6.3	11.7	12.2	11.0	7.8	5.3
Study Site - Recorded	---	11.5	12.1	11.1	---	---
1975						
Edson	7.8	11.4	16.7	11.0	10.1	2.4
Study Site - Predicted	7.4	10.5	15.0	10.1	9.3	2.4
Study Site - Recorded	6.2	9.7	15.1	10.2	7.9	1.2

sheltered Feather moss site. On average the air temperature at the *Tomenthypnum* site was 2.8°C (maximum about 4.5°C) warmer during the day and 1.5°C (maximum about 3.5°C) colder at night than at the Feather moss site. This reduced temperature amplitude at the forested site is similar to the 4°C difference reported for spruce forest by Barkman (1958, p.26). A ten-day period from 25 July to 3 August 1975 was chosen to represent a period with a mean temperature (13.3°C) close to the summer maximum (see Fig. 6) and hourly mean values for this period for both sites are shown in

Fig. 7.

Maximum and minimum temperatures at the study site generally occur at 1600 and 0600 hr respectively. The ameliorating effect of the tree canopy at the Feather moss site results in higher minimum temperatures, the delayed temperature rise in the morning to a lower maximum, and a more gradual temperature decrease in the evening due to a lower rate of energy loss through long-wave radiation (see also Geiger 1966, p.320).

Rates of temperature change at the Tomenthypnum site can be quite rapid. On 13 September 1975, for example, temperature rose from -1.5°C at 0800 to 23°C at 1400, a rise of 24.5°C in six hours. Rates of change of up to 6°C per hour have also been recorded. Such rates may have important physiological implications, particularly when increased by solar radiation.

The information presented here should prove useful in establishing controlled environment conditions for further work. It should be possible to use Fig. 7 in conjunction with Fig. 6 to simulate the temperature for either T. nitens or the Feather mosses at any part of the season.

Moss Temperature

Variation in air temperature at each site, both seasonal and diurnal, has been outlined above. Insight into moss physiological processes, however, requires information

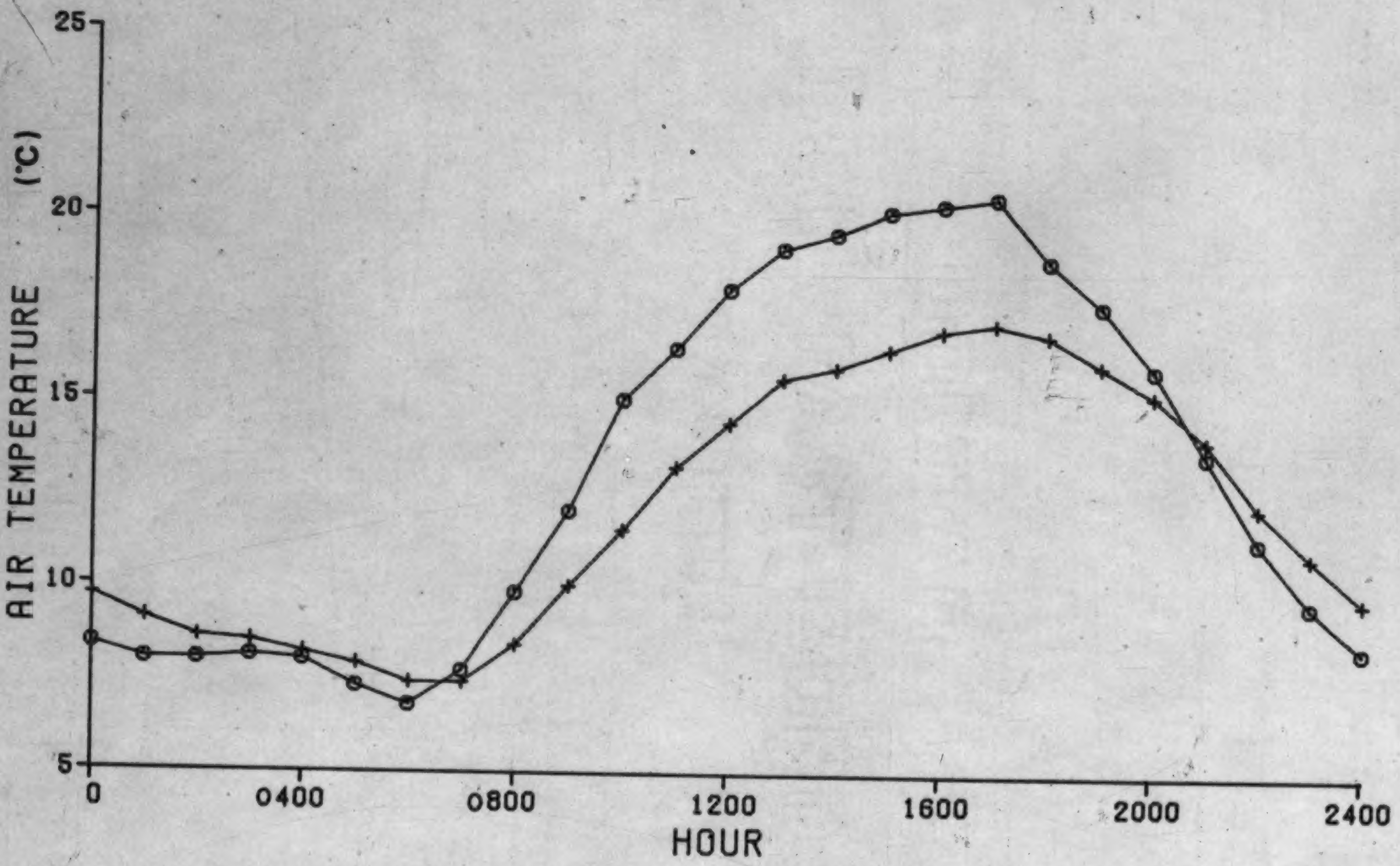
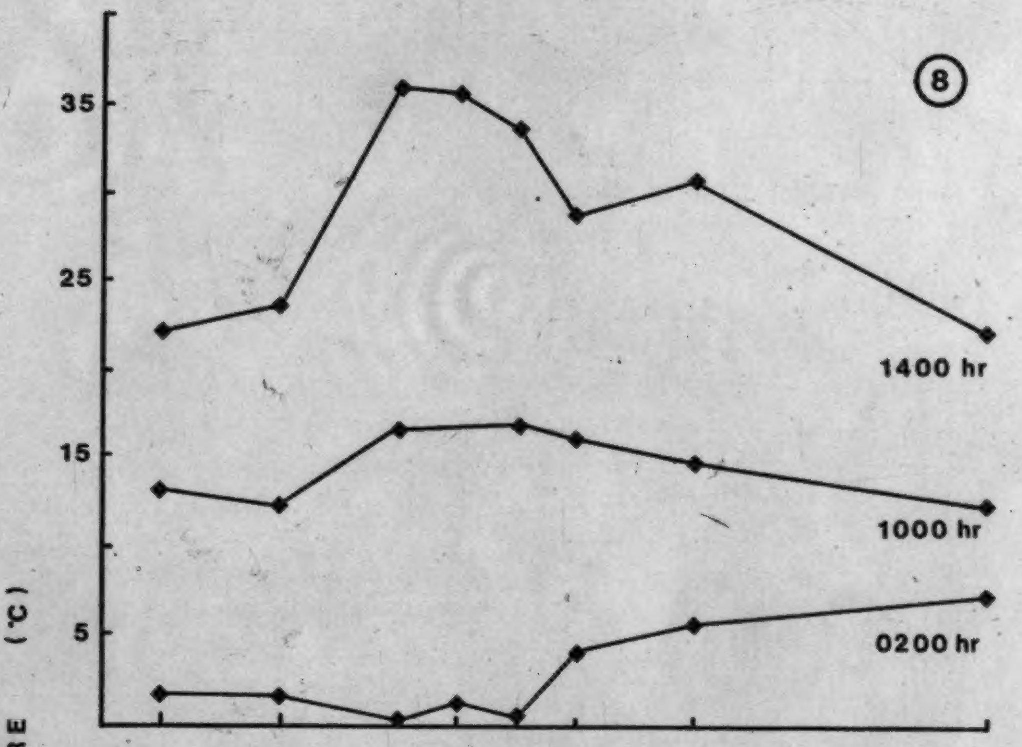


Figure 7. Mean hourly air temperatures for the period 25 July to 3 August 1975: O = Tomenthypnum site; + = Feather moss site.

on the actual tissue temperatures at these times. A series of measurements of temperature profiles in the air and moss at both sites were made at 30 min intervals for a total of 12 days in July and early August 1974. Air temperatures were measured at 25 cm and 3 cm above the moss canopy with very fine (0.005 inch) copper-constantan thermocouples connected through a cold junction compensator to a millivolt recorder. Canopy surface temperatures and temperatures at 1, 2 and 3 cm below the surface were measured by averaging the readings from three similar thermocouples, which were carefully attached to the moss stems by spring-steel clips (after Addison 1973) so that the junctions were in contact with moss tissue. Thermocouples of this size were used in order to reduce effects of solar radiation on the measurements. Radiation effects were assumed to be negligible below 3 cm so temperature measurements at depths of 5 and 10 cm below the canopy surface were made by averaging the readings of three coarser thermocouples situated at each level.

An "average" day was selected for the Tomenthypnum and Feather moss sites, and temperature profiles at three selected times are illustrated in Figs. 8 and 9 respectively. The day chosen to represent measurements at the Tomenthypnum site was 31 July 1974. The diurnal temperature range was typical for that time of year (see Fig. 6), ranging from a morning low of 0°C at 0130, through an afternoon maximum of 23.4°C at 1430, to a minimum evening



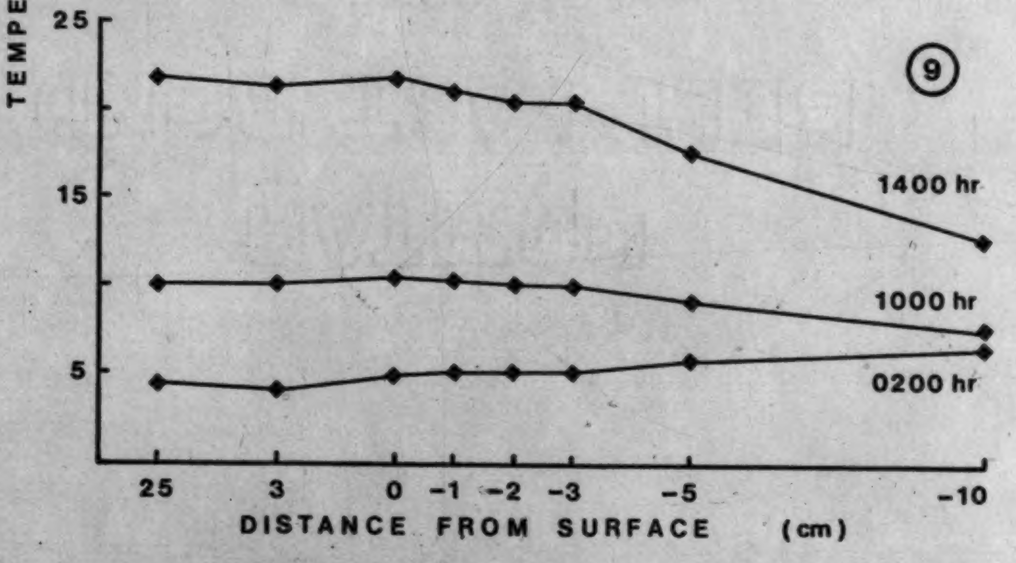


Figure 8. Selected air and moss temperature profiles at Tomenthypnum site, 31 July 1974.

Figure 9. Selected air and moss temperature profiles at Feather-moss site, 2 August 1974.

temperature of 0.3°C at 2400 hr. Examination of the profile for 0200 hr in Fig. 8 shows that the moss surface temperature was depressed below the air temperature. Net radiation at the canopy surface at this time was -0.03 cal cm^{-2} min^{-1}, so the temperature depression indicates a loss of energy by long-wave radiation. During the day the situation was reversed and, at high net radiation levels, the moss temperature was considerably elevated above the air temperature. This is illustrated by the temperature elevation of about 4°C at 1000 hr when the net radiation at the canopy surface was 0.24 cal cm^{-2} min^{-1}, compared with an elevation of 13°C at 1400 hr when the net radiation was 0.88 cal cm^{-2} min^{-1}. It is apparent that the mosses are subjected to rapid temperature fluctuations (cf. Barkman 1958, p.62; Longton 1970, 1972a,b, 1974a). Rates of change of up to 10°C in 30 min have been recorded, with a temperature change in one case from -2.9°C at 0630 to 36.8°C at 1230 on 1 August 1974, nearly 40°C in six hours. The highest canopy surface temperature recorded during the measurement period was 44°C, but higher values and more extreme temperature changes are probably common (cf. Nørgaard 1951). Since the growing point is the stem apex which is at the canopy surface, it is clear that information on the effects of these parameters on the physiology of the moss is required.

Other points to note in Fig. 8 are that variation in temperature at -10 cm is less than the variation in air temperature, and that there is a more or less uniform gradient in moss temperature from the surface to -10 cm (cf. Nørgaard 1951, Longton 1972b).

The day chosen to represent measurements at the Feather moss site, 2 August 1974, was also typical for that time of year. Air temperature ranged from a morning low of 2.4°C at 0400, through an afternoon maximum of 23.4°C at 1630, to an evening minimum temperature of 10.3°C at 2400 hr. The main feature to be seen in Fig. 9 is the shallowness of the temperature profiles, even during the middle of the day. Presumably the moss temperature increases sharply if the moss is directly illuminated by the sun, but no measurements of this were attempted. The temperature at -10 cm again shows less variation than the air temperature.

Moss temperature at a depth of 10 cm was measured at two locations at the _Tomenthypnum_ site during the entire 1975 study period using a Moeller Distance Recording Thermograph which had been calibrated against a mercury thermometer. Five-day mean temperatures were calculated for each of the probes and the average values are illustrated, along with the mean air temperatures for 1975, in Fig. 10. Significant features are that the mean -10 cm temperature track the mean air temperature quite closely, but the -10 cm means do not reach the same values as the mean air temperature until late August (cf. Heinselman 1963). Temperatures were also measured at the -10 cm level at the Feather moss site by a second Moeller Thermograph from 1 May

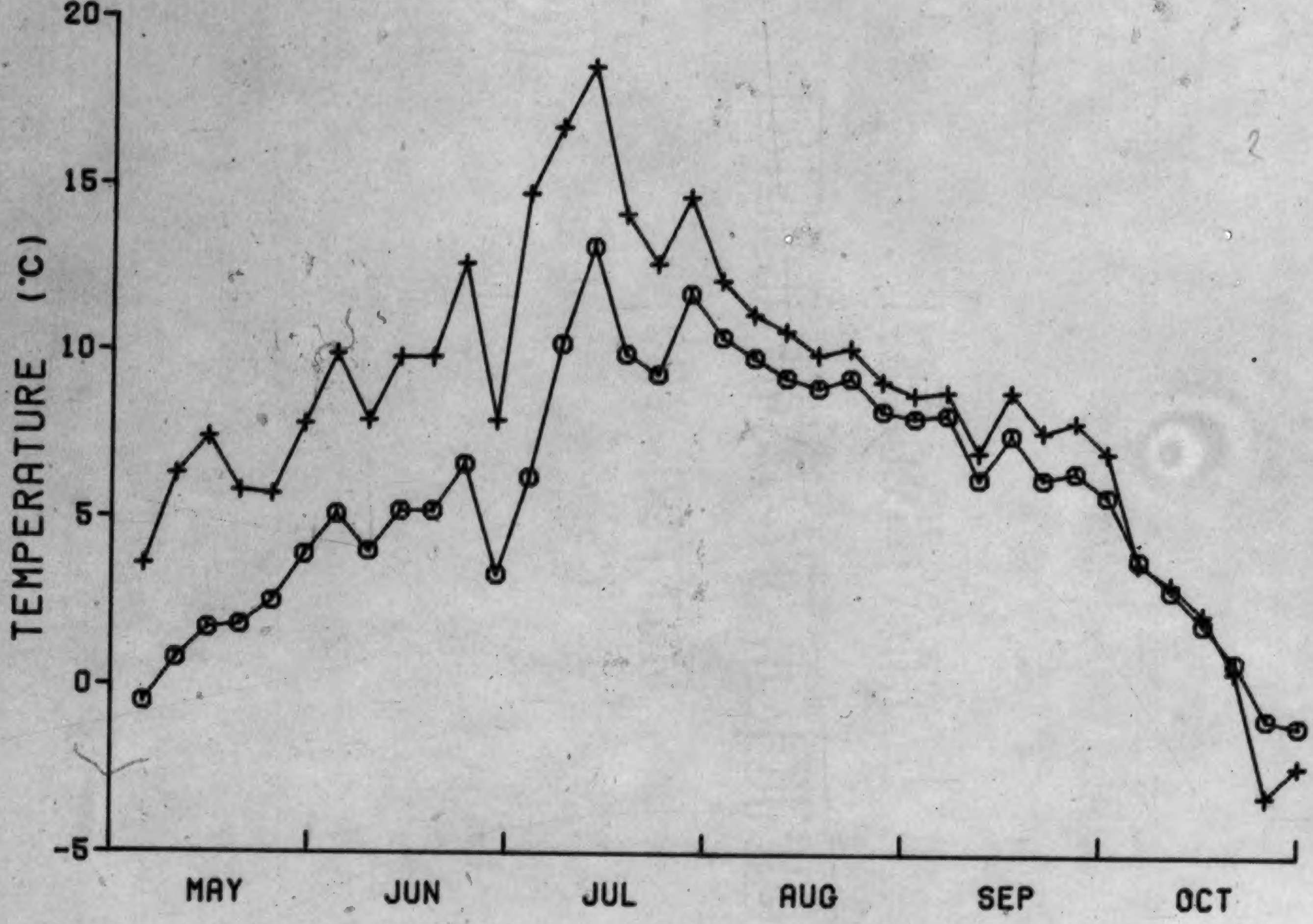


Figure 10. Five-day mean temperatures at Tomenthypnum site in 1975: += air temperature at 5 cm; O = temperature 10 cm below moss canopy surface.

to 3 August 1975. The data from this site showed a pattern very similar to that at the Tomenthypnum site. The temperature at -10 cm was lower than the air temperature for much of the season. The mean soil temperature at -10 cm exceeded 1[illegible]°C only during July and part of August, and during most of May and October the maximum temperature at -10 cm was less than 10°C. This would be expected to have significant implications for decomposition rates and rates of peat accumulation (cf. Weetman and Timmer 1967).

Air Humidity and Evaporation Stress

Relative humidity was measured at the Tomenthypnum site from 1 May to 1 November 1975, and at the Feather moss site from 1 May to 3 August 1975. Measurements were recorded by the Belfort Hygrothermographs described above. The humidity sensors had been calibrated against a sling psychrometer in a controlled environment chamber and this calibration was checked weekly in the field using a sling psychrometer at the same height as the sensor. The agreement between the hygrothermograph and the sling psychrometer averaged 5 relative humidity units (%).

Maximum daily relative humidities averaged 83% at the Tomenthypnum site with minimum values averaging 45%. Relative humidities at the Feather moss site averaged 80% and 49% respectively. No seasonal trends in relative humidity could be discerned.

Relative humidity values, *per se*, are not particularly useful indicators of evaporation stress (Barkman 1958, p.69). A more appropriate estimate of this parameter is the saturation deficit or water vapour deficit, which is the difference in vapour pressure between the actual vapour pressure and the saturation vapour pressure at the same temperature. Vapour pressure deficits were therefore calculated for every hour during the measurement period for each site, and these hourly values were averaged for five-day periods. These mean values were then averaged for 4 six-hour periods and the seasonal trends at the *Tomenthypnum* site in two of these periods, *viz* 0100 to 0600 hr and 1300 to 1800 hr, are illustrated in Fig. 11. The values for 0700 to 1200 hr and 1900 to 2400 hr were intermediate between the others and are not shown. Examination of Fig. 11 shows that there is considerable seasonal variation in water vapour deficit during the hours 1300 to 1800. On the other hand the values for the hours 0100 to 0600 show little seasonal change. Mean water vapour deficits from 1300 to 1800 hr at the Feather moss site averaged 80±3% (mean±s.e.) of those at the *Tomenthypnum* site. Site differences can be attributed to air temperature differences.

Water vapour deficit is, however, only one component of evaporation stress, the other major components being solar radiation and wind. Seasonal trends in evaporation stress are best established, therefore, by measuring evaporation directly. This was done at the *Tomenthypnum* site from mid-

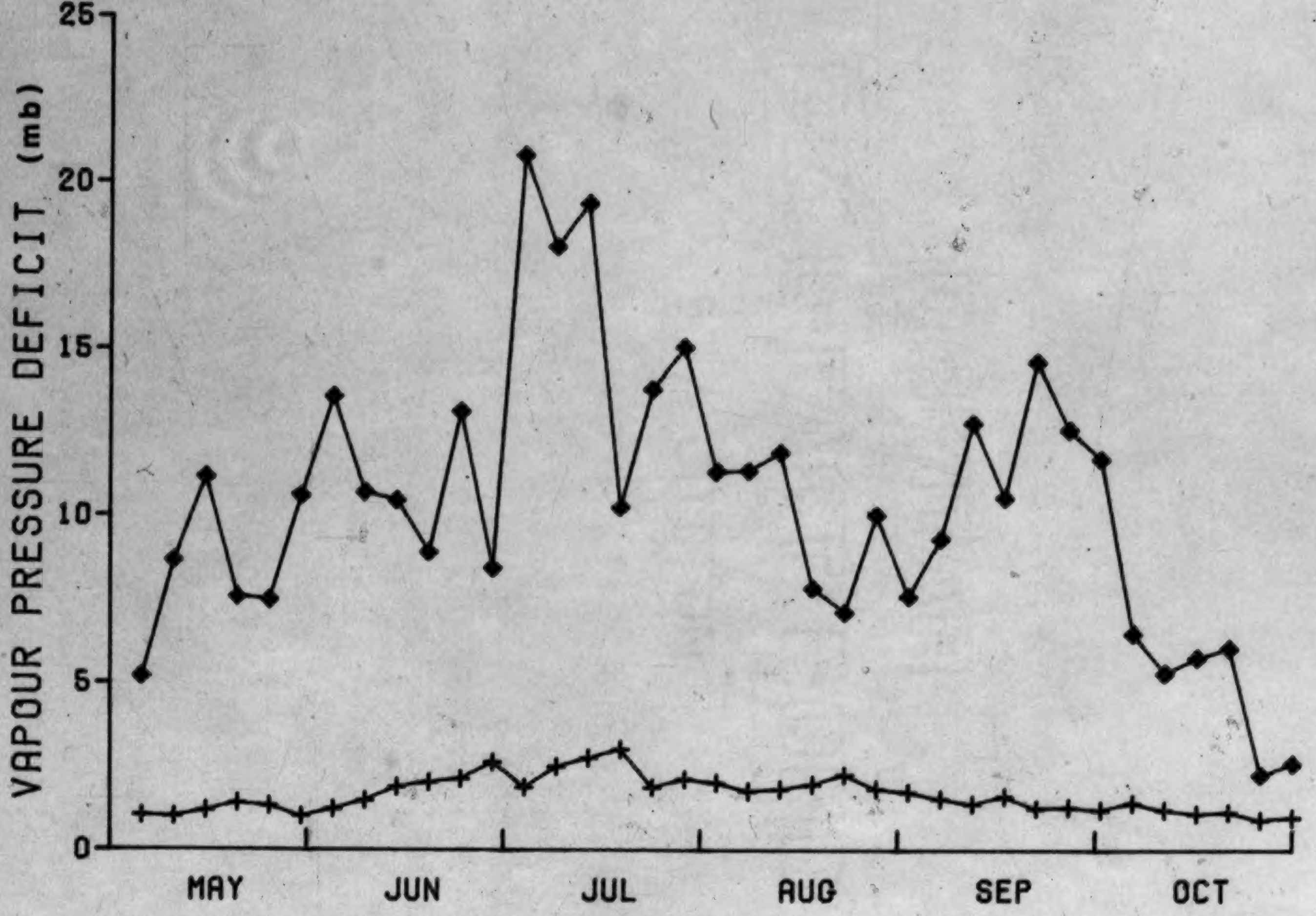


Figure 11. Five-day means of vapour pressure deficit at Tomenthypnum site in 1975: ◆ = 1300-1800 hr; + = 0100-0600 hr.

June to late October using an "Evaporation Gage" (Model E-801, Weather Measure Corp., Sacramento, California). This instrument measures water loss from filter paper (Whatman No. 2) and was calibrated in the laboratory to measure evaporation in units of mm water per unit time. Daily evaporation totals were calculated and averaged over half-month intervals (Fig. 12). Finer resolution of the data was not possible because rainfall frequently forced the instrument off scale and many daily totals were lost as a result. A comparison of Figs. 11 and 12 shows a close relationship between measured evaporation and water vapour deficit. The apparent exception in mid to late September will be discussed below.

Evaporation at the Feather moss site was measured by a second Evaporation Gage. Daily evaporation rates averaged 57% of those recorded at the Tomenthypnum site. Measurements made at other sites where Feather mosses were predominant showed similar proportions. The evaporation rates in the forest compared with the open are higher than the 20-30% reported by Birse (1958b) for deciduous forest and the 27-52% range for forests reported by Barkman (1958, p.25). This may be a consequence of higher water vapour deficits than in the maritime climates of the regions studied by Birse and Barkman, or the absence of a significant shrub layer which allows greater air circulation (cf. Potzger 1939; Barkman 1958, p.25).

The nature of the differences in evaporation rates

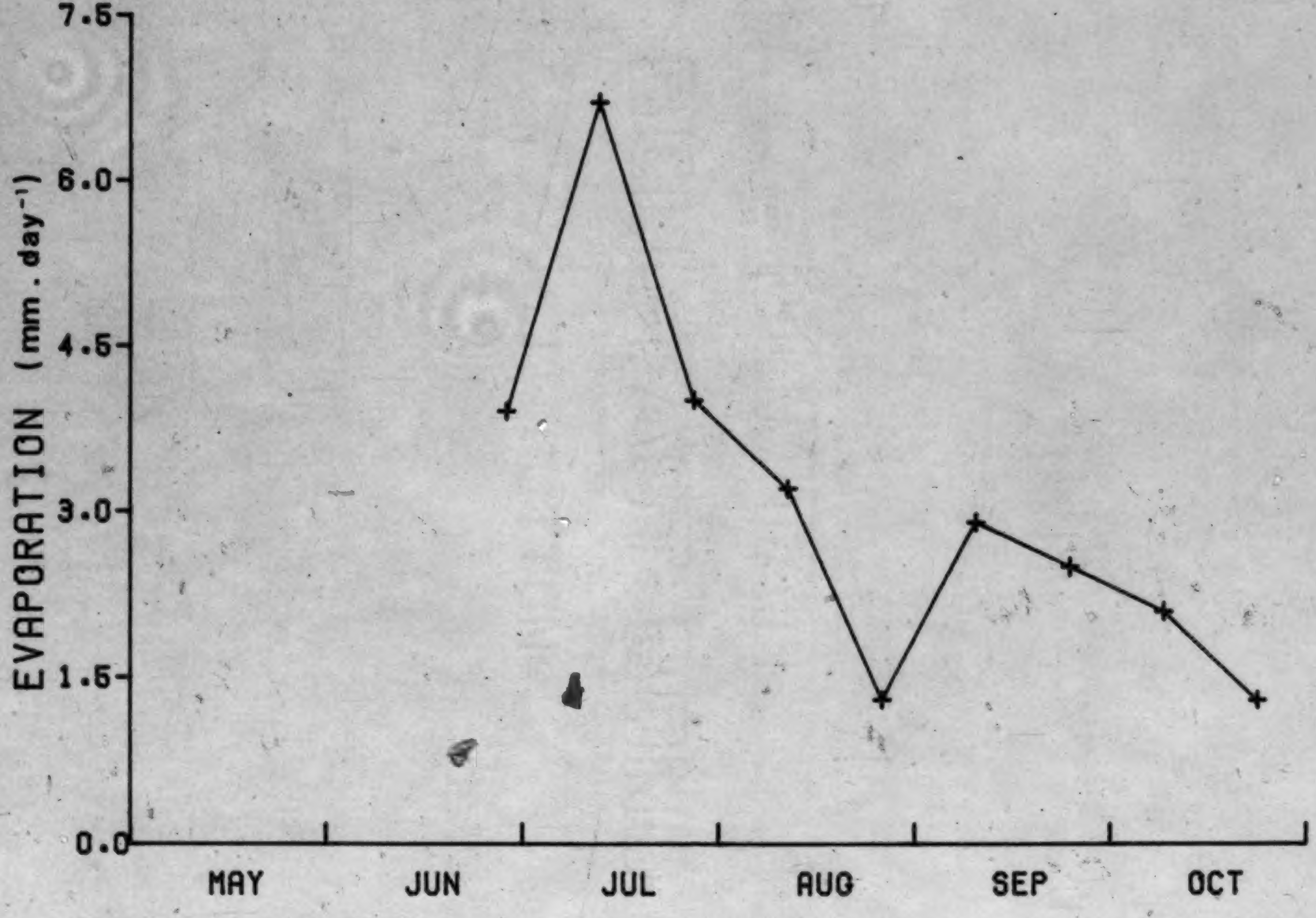


Figure 12. Mean daily evaporation at Tomenthypnum site in 1975. Data represent water loss from Whatman No. 2 filter paper.

between the Tomenthypnum and Feather moss sites can be demonstrated by the diurnal patterns in this parameter. These patterns were established for the period from 15 June to 15 August 1975 as follows: for each day at each site, evaporation during successive two hour periods was expressed as a percentage of the maximum value measured during any two hour period at either site on that day. These percentages were averaged and the means and standard errors for each two hour period are shown in Fig. 13. Examination of this Figure shows that evaporation is very low from midnight until 0900 hr, with the Feather moss site showing higher values than the Tomenthypnum site. Comparison of this Figure with Fig. 14, which illustrates the mean hourly water vapour deficits for both sites for the period 1 May to 3 August, shows that evaporation pattern at the Feather moss site is closely correlated with the diurnal pattern in water vapour deficit.

Evaporation at the Tomenthypnum site, on the other hand, shows a different pattern. The peak in evaporation at 1300 hr can probably be attributed to solar radiation reaching a maximum at that time (Geiger 1966, p.255), and the decline during the afternoon reflects the decrease in radiation. The values are higher after than before 1300 hr because water vapour deficit at the Tomenthypnum site reaches a maximum at 1600 hr (Fig. 14). It should be noted that evaporation rates at the two sites are equivalent when the water vapour deficits cross over at about 2100 hr. An

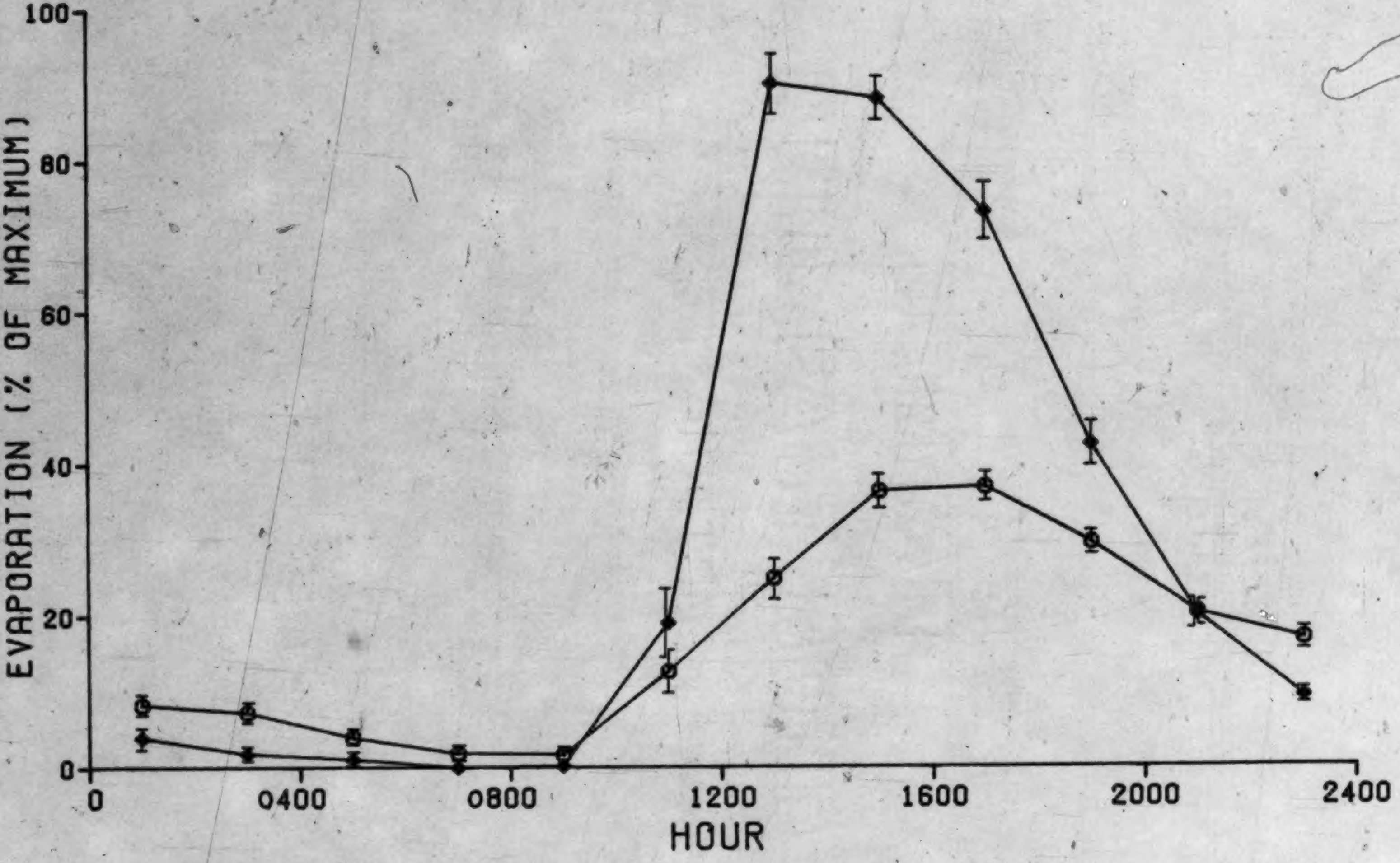


Figure 13. Mean diurnal pattern of evaporation from 15 June to 15 August 1975: ◆ = *Tomenthypnum* site; O = Feather moss site. Values shown are mean percentages of daily maximums ± standard errors.

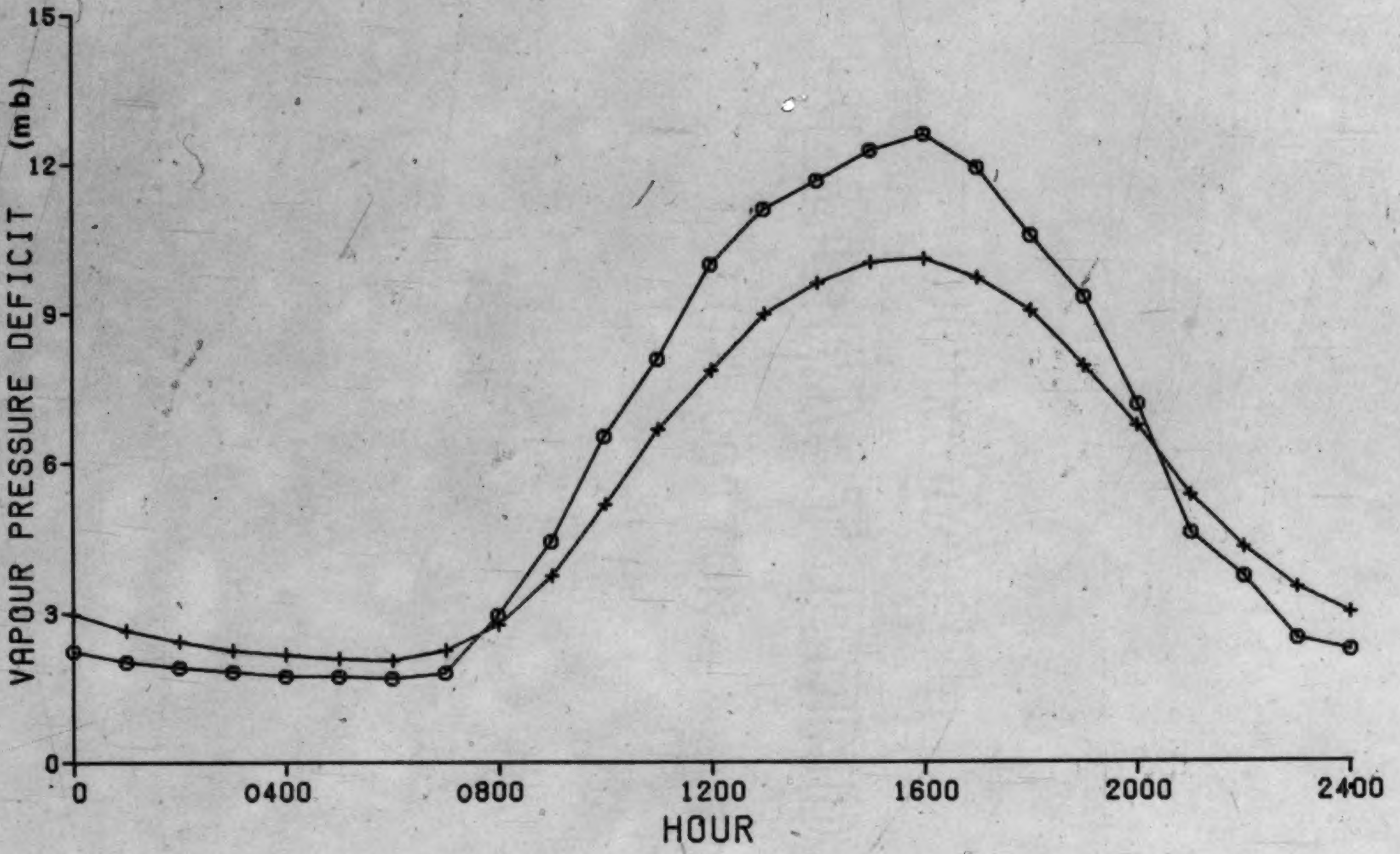


Figure 14. Mean hourly water vapour deficits for the period 1 May to 3 August 1975:
O = *Tomenthypnum* site; + = Feather moss site.

Table 3. Mean monthly wind speeds at Tomenthypnum site in 1975.

Month	Mean Wind Speed ($m\ sec^{-1}$)
May	0.27
June	0.18
July	0.10
August	0.08
September	0.08
October	0.10

additional feature is the apparent delayed rise in evaporation rate at both sites in the morning. The water vapour deficit rises after 0700 hr but the evaporation rate shows no increase until after 0900 hr. This delay may be due to low morning wind speeds, but this remains to be confirmed since no wind speed measurements were made at that time.

Figs. 13 and 14, therefore, give some indication of the relative effects of water vapour deficit and solar radiation on evaporation stress at the two sites. Wind, which will be discussed later, is probably a factor in the increased afternoon evaporation rate, but it was not possible to quantify this effect. The evaporation rates recorded during mid- to late-September, mentioned above, which were lower than would be expected from the water vapour deficit data

(Fig. 11, p.51) might be attributable to a combination of low radiation levels (Fig. 4, p.27) and low wind speeds (Table 3).

Precipitation

Rainfall was measured at the _Tomenthypnum_ site by a Belfort Recording Rain Gauge from 10 June to 17 September 1974 and from 1 May to 22 October 1975. The instrument was placed in the open, well away from trees, and the rainfall totals for five-day periods are shown in Fig. 15. It is apparent that rainfall is frequent throughout the season, although the total amounts probably decline in late September and October (cf. Fig. 3, p.25). Precipitation during September and October is occasionally in the form of snow. Light snow was noted in early September 1974 and heavier snow falls occurred after 22 October 1975. The rain gauge was not appropriate for measuring snowfall so no precipitation records were made for that period. Snow which falls at that time of the year is rarely persistent, usually melting within a few days.

Rainfall appears to be associated with weather systems which last for two or three days, these systems being separated by rain-free periods of four to five days. There is, of course, considerable variation and rain-free periods of more than a week can occur at any time during the season. The long-term mean monthly rainfall for July at Edson is

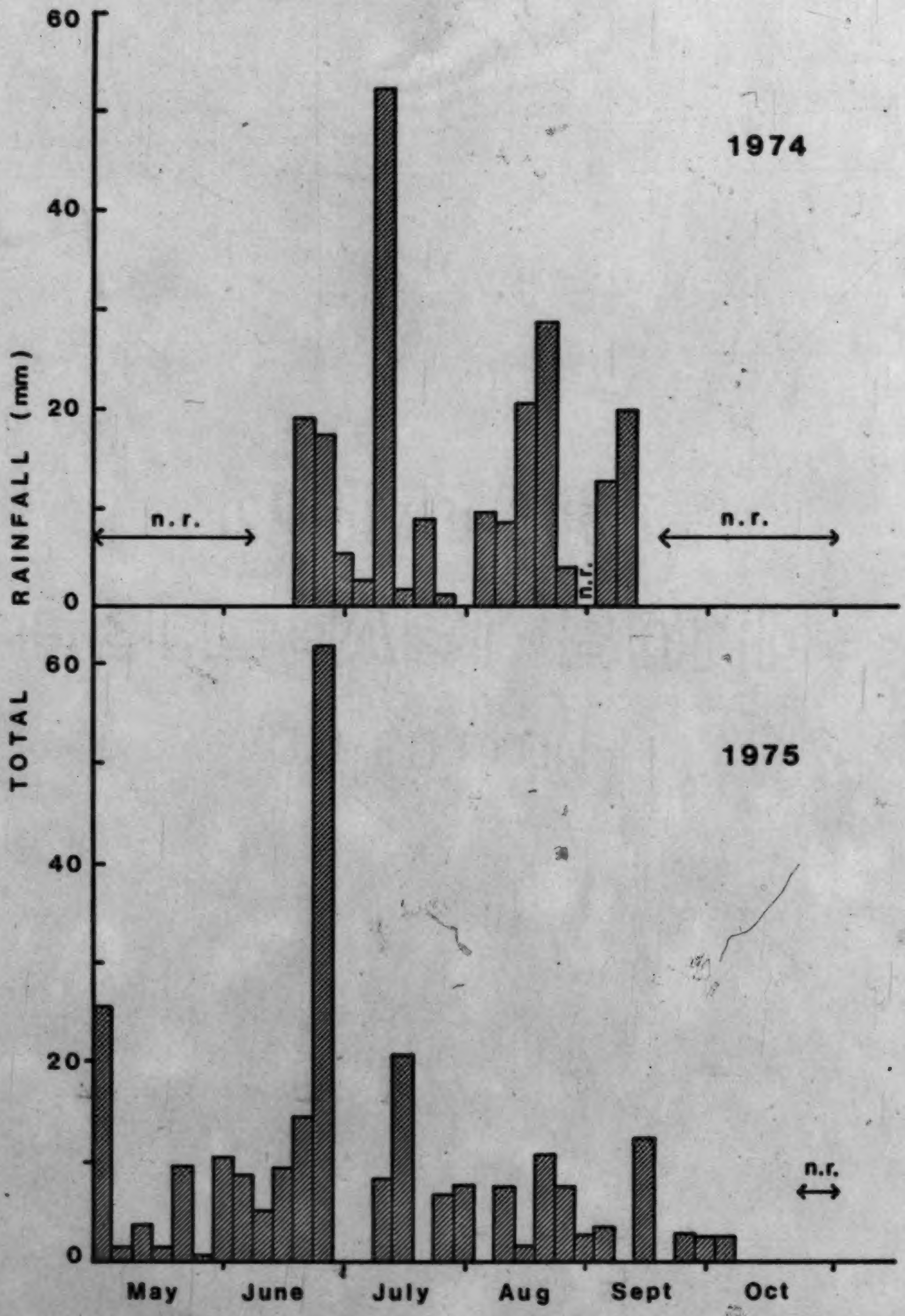


Figure 15. Five-day rainfall totals at Tomenthypnum site: n.r. = not recorded.

over 100 mm, yet a rain-free period exceeding 12 days was recorded at the field site during July 1975.

Rainfall occurs most frequently in the early morning and evening. The evening rainfall frequently is derived from thunderstorms which are a common consequence of the afternoon cloud build-up discussed earlier. The intensity of this rain tends to be quite high and the period from 1800 to 1900 hr accounts for nearly 10% of the total rainfall recorded during the measurement periods in 1974 and 1975.

There was a low correlation between rainfall recorded in 1974 and that recorded at Edson, probably due primarily to the localized nature of the thunderstorms during the summer. No attempt was made, therefore, to use the Edson data to extend field observations or to compare 1974 and 1975 precipitation values with long-term means.

The patterns of rainfall received by the Feather mosses were investigated using small plastic "Tru-Chék" rain gauges (Edwards Mfg. Co., Albert Lea, Minnesota). A total of 70 readings was taken during 1974 and 1975 at various locations and it was found that rain falling on the Feather mosses averaged 78% of that received in the open. This value is similar to the 66% recorded by Abolin' (1974) for a Pinus - Feather moss forest in the U.S.S.R. and with 73% reported by Schubert (1917, cited in Barkman 1958, p.26). A frequency distribution (Table 4) shows that the variation was considerable, with values ranging from 19% to 132%. Field observations indicate that rainfall received by the Feather

Table 4. Frequency distribution of the percentage of rainfall reaching the Feather moss canopy compared with the open. Mean throughfall = 78%.

Throughfall (%)	Number of Observations
>110	1
101-110	7
91-100	20
81-90	11
71-80	8
61-70	7
51-60	8
41-50	3
31-40	2
21-30	2
<20	1
Total	70

mosses depends not only on location relative to the tree canopy but also on the duration and intensity of the rain (cf. Geiger 1966, pp.326-336; Weetman and Timmer 1967). Light rain in the order of 1 mm or less was almost entirely intercepted by the Picea mariana canopy and only mosses growing in relatively open situations were wetted (cf. Geiger 1966, p.328). The proportion of rainfall penetrating the tree canopy increased with the amount of rain to the extent that penetration values of around 100% were achieved when precipitation was in the order of 20 mm.

Wind

Wind was recorded at the two sites by Belfort 3-cup Totalizing Anemometers, the cups of which were located at a height of 25 cm above the moss canopy surfaces. A calibration period of five weeks showed that the average agreement between instruments was within 5%. The objectives were to record the seasonal patterns in wind speed and to compare the wind speed over _T_. _nitens_ with that over the Feather mosses. The average wind speed for each month was calculated and the data for the _Tomenthypnum_ site are shown in Table 3.

Observations in the field using a Hastings Model AB-27 Air-Meter with a directional probe indicated that wind speeds less than about 0.3 m sec^{-1} were not recorded by the anemometers. Table 3 shows that the average monthly wind speeds at the _Tomenthypnum_ site were all less than this value, which means that the wind speeds are almost certainly under-estimates of the true values. It is apparent, however, that there was more wind in May and June than during the other months.

Wind was measured for 15 weeks at the Feather moss site and for 4 more weeks at another site dominated by Feather mosses. The amount of wind recorded at these sites varied from 12% to 35% of that recorded at the Tomenthypnum site for the same periods. The actual magnitude of this difference, however, is uncertain due to the problem outlined above, but it seems clear that trees reduce the wind velocity over the Feather mosses compared with that over T. nitens. More accurate instruments would be required to quantify this difference.

Wind speed at the canopy surface would be expected to be lower than at 25 cm above the surface due to friction effects of the moss canopy (cf. Barkman 1958, p.26). More than 300 wind profile readings were taken throughout the 1974 season in various weather conditions at both the Tomenthypnum and Feather moss sites and it was found that wind speed at the canopy surface averaged about 20% of the wind speed at 25 cm, with no significant differences between the sites.

III. FIELD GROWTH RATES

1. Methods for Measuring Bryophyte Growth

The most comprehensive treatment of methods for measuring bryophyte growth rates is that of Clymo (1970). Clymo divided methods of measurement into four categories:

a) The use of innate time markers, i.e. natural cyclic changes of branch length and spatial density of branches.

b) The use of reference markers outside the plant, i.e. measurement of length increase against external reference marks.

c) The measurement of growth of plants cut to known initial lengths.

d) Direct estimates of changes in weight.

Innate time markers have been used successfully in measuring the growth rates of Hylocomium splendens (Tamm 1953), Polytrichum alpestre (Longton 1970, 1972c), Aulacomnium palustre (Reader and Stewart 1971, Teczynska-Kamecka 1974), Pohlia wahlenbergii var. glacialis (Clarke et al. 1971), and Polytrichum strictum (Longton 1974b). Annual shoots, corresponding to those of Hylocomium splendens, can sometimes be distinguished in Pleurozium schreberi and Ptilium crista-castrensis (Tamm 1953, p.39), and growth of Pleurozium schreberi has also been estimated from gametangial position and from the morphology of the apical region (Longton and Greene 1969). Growth of the Feather moss species, particularly Hylocomium splendens, can therefore be estimated fairly readily by using this approach.

An examination of samples of Tomenthypnum nitens from the study site, however, revealed no consistent cyclic fluctuations, so it was not possible to use annual shoots to measure the growth rate of this species. This was also the case in a majority of 42 samples of Sphagnum collected by Clymo from a variety of sites in England. Even when cyclic changes were observed it was possible that the changes were not necessarily seasonal but reflected abrupt changes in temperature or water supply, or both (Clymo 1970).

Overbeck and Happach (1956, cited in Clymo 1970) used a thread tied round the stem as a marker against which to measure growth of Sphagnum plants. This was unsuccessful, however, in habitats which were not fully aquatic. The monthly measurements caused the plants to dry out since it was impossible to effectively rearrange them into their natural orientation. Clymo (1970) also attempted to use this method but soon abandoned it. Due to the lack of success with this method in these studies, no attempt was made to use thread markers to measure growth in Tomenthypnum nitens.

A more successful method of using external markers to measure bryophyte growth was described by Clymo (1970). It involves the use of

> "... many separate cranked stainless steel wires (shaped like a car starting handle). One end of the wire, which can conveniently be about 10 cm long, is pushed into the *Sphagnum* carpet vertically... The horizontal section, about 1 cm long, is level with the capitula, whilst the free end, which must be of exactly known length, projects into the air.
>
> "The *Sphagnum* plants grow up around the vertical free end of the wire and the growth is measured from the amount of wire still projecting above the surface. The cross piece increases resistance to vertical movement of the wire among the plants."

This "cranked wire" method, which provided useful results in Clymo's study, has also been used successfully in studies by Sonesson (1973) and Sonesson and Johansson (1973). It was used in this study to measure growth in *T. nitens*.

Measurement of length increments in plants cut initially into known lengths and then replaced in the mat has been criticized by Clarke *et al*. (1971) on the basis that this procedure is likely to affect natural growth processes. Clymo, for example, found "... some indication that the growth in length is inversely related to the initial length and quite strong indication that growth in weight is similarly related." This could be particularly significant when growth rates are very low.

Despite this problem, field testing of a modification of this approach, the "capitulum correction" method (see Clymo 1970), has provided quite accurate measurements of growth with some *Sphagnum* species. Some preliminary investigations of the feasibility of using this method to measure the growth of *Tomenthypnum nitens* were made. The morphology of individual stems of this species, however, is so variable that the requirement for a close correlation between the weight of the top 1 cm (the capitulum in *Sphagnum*), and of the next 3 cm of stem with the branches removed, was not met (these, and all subsequent weight determinations, were made using a Mettler Type H6T analytical balance). Correlation coefficients for the *Sphagnum* species measured by Clymo (1970) ranged from 0.84 to 0.97, whereas those for the three samples of *T. nitens* measured in this study ranged from 0.74 to 0.81. The capitulum correction method, therefore, was not used to measure the growth of this species.

Weight differences between samples collected from the field at different times cannot be used to estimate growth of *Tomenthypnum*, because of the considerable variation in weight for plants of equal length, the low growth rates, and the difficulty of interpreting the relationship between green, non-green and dead tissue.

2. Growth of *Tomenthypnum nitens*

Length increments of *T. nitens* were measured from early May to mid-October 1975 using the cranked wire method outlined above. Ten sites in the fen (veg. type C, p.16) were arbitrarily selected and, at each site, five wires were carefully inserted into the moss mat so that the horizontal cross pieces were level with the moss surface. Each wire consisted of an 8 cm basal portion, a 1 cm cross piece, and a 2 cm upright which projected vertically above the surface (Plate 3b). The sites were visited at approximately monthly intervals and length increments of the moss stems relative to the wires recorded.

Within three weeks it was noted that the rates of length increase were quite variable, and that this variation was correlated with the colour of the apical region. At each subsequent measurement period, therefore, the colour of the apical region of the moss was noted along with the length increment. Four colour categories were established, _viz_ brown, yellow-brown, yellow-green and green, and length increments for the samples in each category were averaged. These values are presented in Fig. 16 which shows that stems with green apices (Plate 3c) had the fastest elongation rates, followed by yellow-green then yellow-brown (Plate 3b). Some of the moss which remained brown during mid-summer (cf. Plate 3a), and which showed no growth during that time, developed green shoots in early autumn and grew some 4 mm in two months.

It was hypothesized that the colour of the apical region was correlated with water content, and that the water contents determined the differences in growth rates. Samples of the top 1 cm of various colours of _T. nitens_ were collected between 1300 and 1530 hr on 2, 9 and 23 July and 14 August 1975, and the water contents determined relative to dry weight at 80°C. For a total of nine samples of each

Plate 3

Colour categories of *Tomenthypnum nitens*:

a) *Tomenthypnum nitens* transplanted to ridge top on 14 May, photographed on 27 August. Sheltered part in upper right corner green, remainder of mat is brown. Size is approx. 30 x 55 cm.

b) Yellow-brown *Tomenthypnum nitens* showing two cranked wires used for growth measurements. Uprights of wires are 2 cm, cross bars are 1 cm.

c) Green *Tomenthypnum nitens* with three cranked wires.

a
b
c

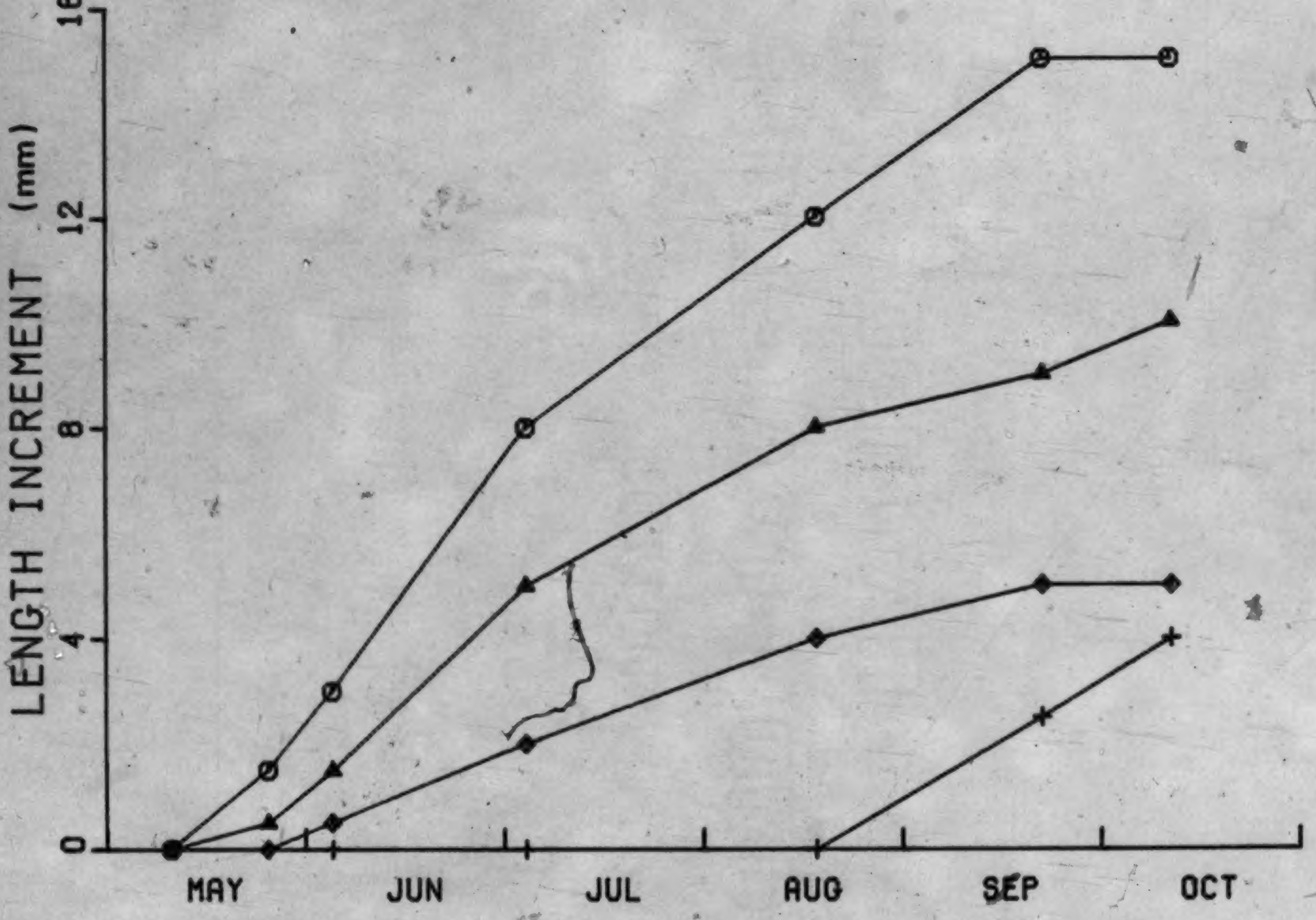


Figure 16. Length increments of the different colour categories of Tomenthypnum nitens in 1975: ○ = green; ▲ = yellow-green; ◇ = yellow-brown; + = brown.

colour, the water contents of moss with green apices averaged 3.44±0.23, that of yellow (yellow-green plus yellow-brown) 2.09±0.14, and of brown 0.35±0.11 g • g dry wt^{-1} (mean±s.e.). The difference between each pair of means is significant to P<0.001. The implications of these results will be discussed later.

3. Growth of Hylocomium splendens

Of the three feather moss species, growth of *H. splendens* is most easily measured because of the sympodial chain of annual shoots (Tamm 1953). Tamm (p.22) suggested that one way of eliminating the problem of the varying size of the moss individuals in different samples is to express the different segments in a sample as a proportion of a certain "base" segment (see also Longton 1970). In this study the segment which grew in 1973 was chosen as the base segment; it is hereafter referred to as the "1973 layer".

Samples of *H. splendens* were collected from the study site at weekly intervals from 30 April to 2 November 1975. In most instances two collections, from different locations, were taken at each sampling time, although in some cases only one, or occasionally three, collections were made. A total of 48 collections was made during the season.

From each collection the first 30 individuals which met the sampling criteria were selected. Individuals were rejected if they were branched at or above the 1972 layer, possessed sporophytes, or were obviously damaged. The 30 selected individuals were then separated into segments and those older than the 1972 layer were discarded. Initially the segments from each stem were weighed individually and the dry weight (80°C) of each was expressed as a proportion of that of the 1973 layer. The 1972 layer was also measured as a check on the 1973 layer since, as Tamm (1953, pp.22-23) pointed out, if the segment selected as the base segment is subject to either growth or decomposition, errors in the figures for the other segments will follow.

The calculation of the ratios for each layer of each stem allowed calculation of confidence limits for the mean ratios of each layer for each sample. It was found that the 95% confidence limits for these ratios averaged about 10% either side of the mean, and rarely exceeded 15%.

It was considered that the first 26 collections provided a reasonable estimate of the confidence limits of the mean ratios. As weighing individual segments was tedious, the procedure for measuring the ratios was simplified by aggregating the segments from each year, obtaining the dry weight, and calculating ratios for the entire sample. The complete data are presented in Fig. 17.

This Figure shows that the choice of the 1973 layer as the base segment was a reasonable one, since there appears to be no significant seasonal change in the ratio between this layer and the 1972 layer. A line of best fit through the points on the 1972 graph, however, shows a slight

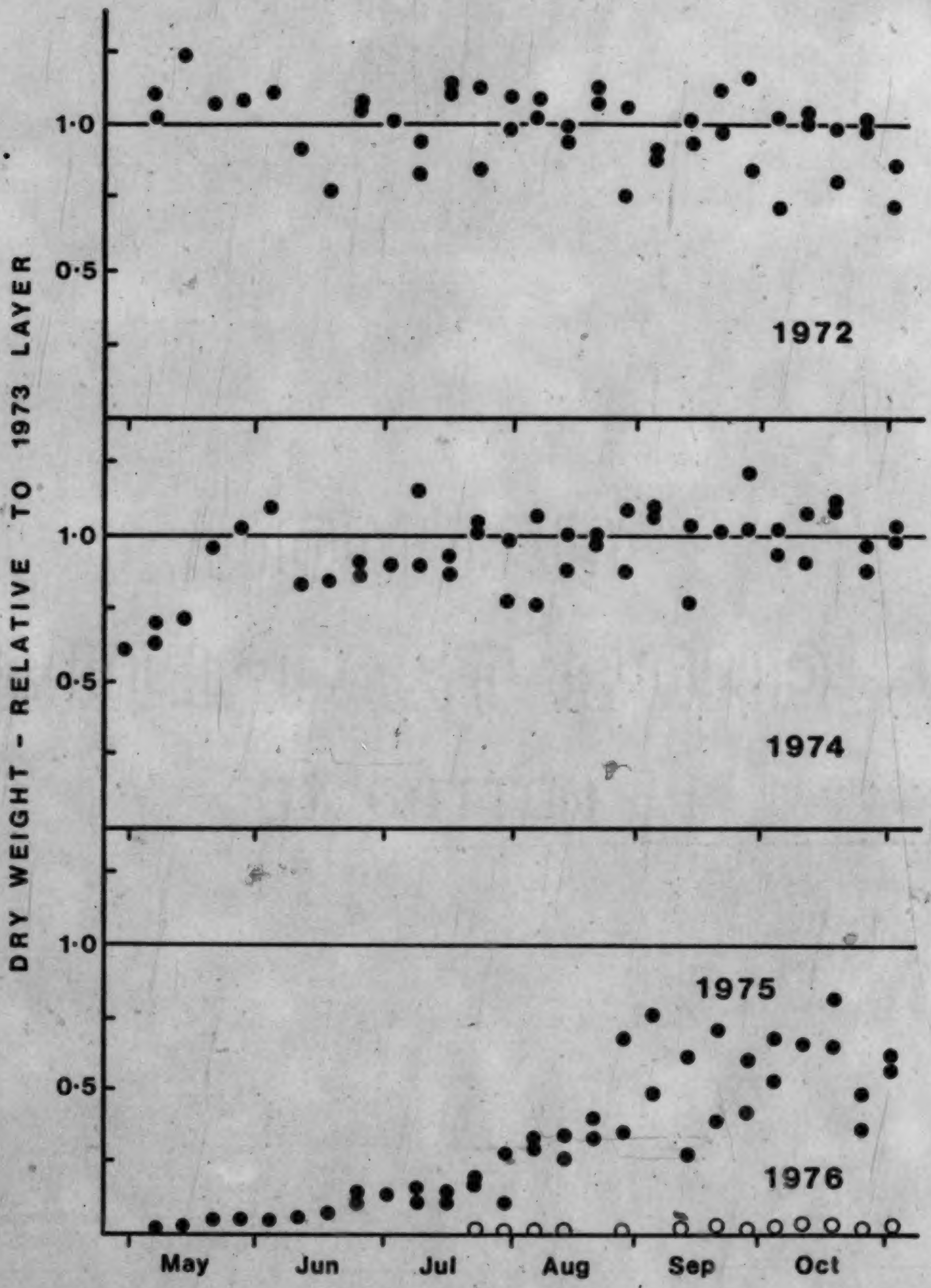


Figure 17. Growth of Hylocomium splendens in 1975. Changes in dry weight of the 1972, 1974, 1975 and 1976 layers expressed as ratios of the 1973 layer.

negative slope of 0.16 units for the six month season. It is suggested that this line may represent decomposition of the 1972 layer because, if the line was continued, it would reach zero in about seven seasons, a value consistent with decomposition rates observed in the field (assuming no significant decomposition during the winter months). This is comparable with an estimate of 5-12 years for decomposition reported by Weetman and Timmer (1967) for Ontario populations of this species.

Growth of the 1974 layer was resumed in the early part of 1975, the relative mass of this layer increasing from 0.6 in early May to 1.0 in mid-June (Fig. 17). A similar phenomenon was observed by Tamm (1953, p.24). It should also be noted that the 1975 layer did not show any significant growth until completion of growth of the 1974 layer.

The 1975 layer grew mainly in July, August, and September. By the end of October the average biomass of the 1975 layer was approximately 60% of that of the 1973 layer, a value which is identical with that of the 1974 layer in early May. This appears to support statements by Tamm (1953, p.20), Longton and Greene (1969), and Longton (1970, 1972b) that there appears to be little, if any, growth activity over the winter months in continental and polar climates.

The future 1976 layer appeared as a small bud in late July, but showed no significant growth during the 1975 season. Its biomass at the end of October was similar to the biomass of the 1975 layer in early May. The cause of this apparent inhibition has yet to be established, although a requirement for cold conditioning seems not to be a factor since material maintained in a controlled environment chamber at temperatures well above 0°C showed rapid growth of the 1976 layer after October.

Up to this point discussion has centred around growth in undisturbed habitats. Removal of the tree canopy is known to kill Feather mosses (Tamm 1953, p.103; Heinselman 1963, Weetman and Timmer 1967), but what effect does the removal of the shrub and herb canopy, the tree layer remaining intact, have on the growth of *Hylocomium splendens*?

A region of the forest floor was selected where the cover of the tree canopy was about 60% and where *Ledum groenlandicum* had a canopy cover of 40-50% over a dense carpet of Feather mosses. *L. groenlandicum* is an erect ericaceous shrub, some 20 to 50 cm high, with elliptic-oblong leaves 3 to 5 cm long which are predominantly clumped at the branch tips. Four areas, each 1 m², were cleared of this and other shrub and herb species. Areas 1 and 2 were cleared in mid-June 1974. The shrub and herb canopy of Area 1 consisted of *Ledum groenlandicum* (35% cover), *Smilacina trifolia* (10%), *Carex aquatilis* (<5%), *Equisetum sylvaticum* (<5%), and *Vaccinium vitis-idaea* var. *minus* (<5%). The shrub and herb canopy of Area 2 consisted of *Ledum* groenlandicum (35%), Equisetum sylvaticum (5%), Smilacina trifolia (<5%), and Vaccinium vitis-idaea var. minus (<5%). Area 3, with a cover of Ledum groenlandicum (45%), Equisetum sylvaticum (5%), and Vaccinium vitis-idaea var. minus (5%), was cleared on 4 June 1975. Area 4, with a cover of Ledum groenlandicum (55%), Cornus canadensis (5%), Smilacina trifolia (5%), and Vaccinium vitis-idaea var. minus (<5%), was cleared on 2 July 1975.

Samples of Hylocomium splendens were collected from the cleared areas at monthly intervals in 1975. Samples were not collected from Areas 3 and 4 until the month following clearing. From each sample collected from each of the cleared areas, 30 stems were selected and the individual segments weighed, as described above. The results are plotted in Fig. 18, superimposed on the data for the 1974 and 1975 layers from Fig. 17.

Figure 18 shows that the 1974 layers from Cleared Areas 1 and 2 had a slower growth rate than those from undisturbed carpets and completed their growth approximately one month later. In contrast, the 1974 layers from Cleared Areas 3 and 4 did not appear to have been affected, presumably because their growth was completed before clearing took place. The 1975 layers from Cleared Areas 1, 2, and 3 also had a slower growth rate, although the 1975 layer of moss from Cleared Area 4 did not appear to have been affected.

It can be concluded, therefore, that the growth of Hylocomium splendens is so closely balanced with its

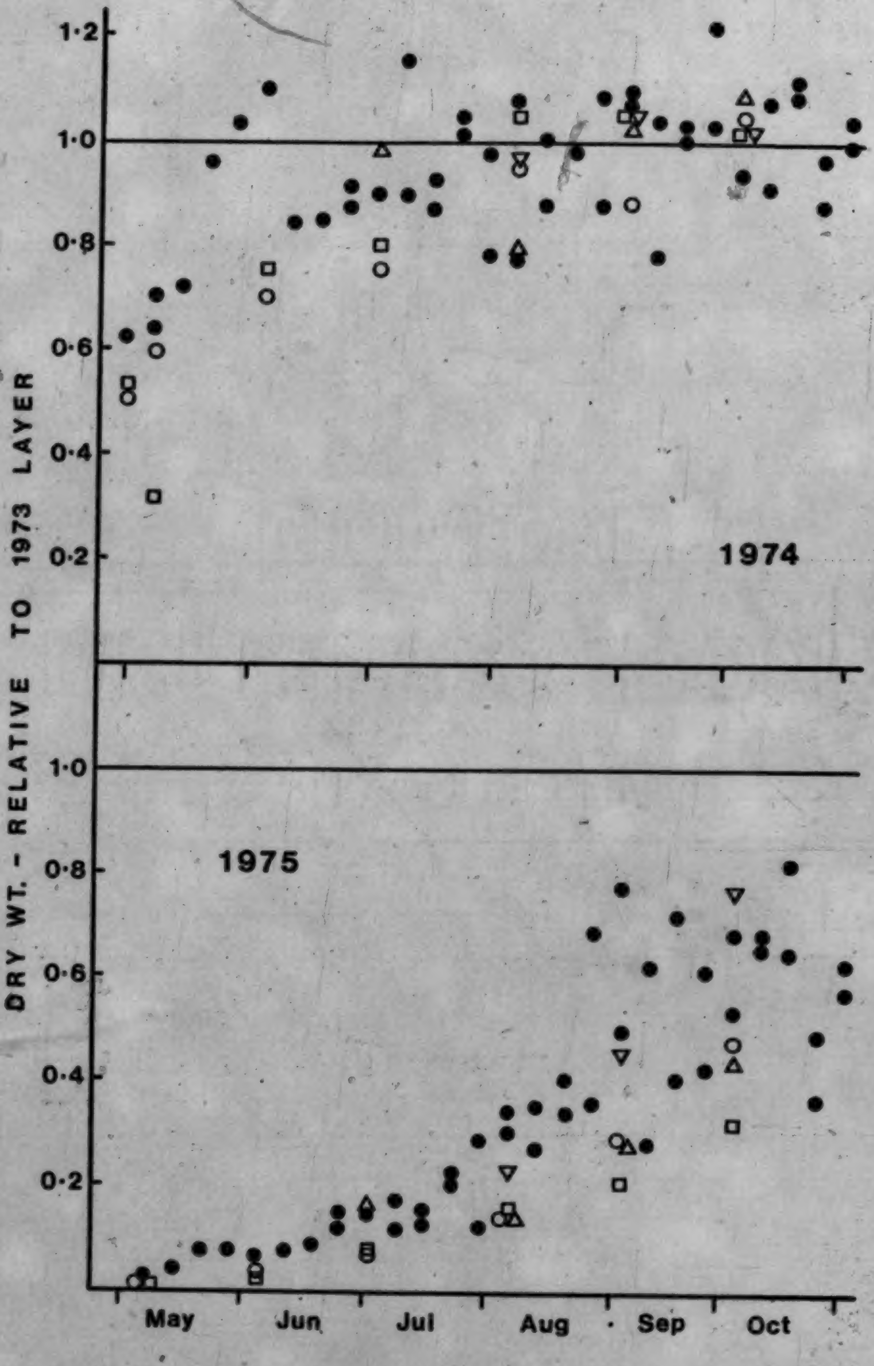


Figure 18. Effect of shrub clearing on growth of Hylocomium splendens: ● = growth of 1974 and 1975 layers in undisturbed areas; open symbols = growth in cleared areas: ○ = area 1, □ = area 2, △ = area 3, ▽ = area 4.

microclimate that even the removal of a rather open shrub layer can have measurable effects on growth rates. These effects are difficult to quantify since the growth of the undisturbed moss is so variable. Some of the factors which might be involved will be discussed later.

4. Productivity of the Moss Carpets

One advantage of the moss system is that there are no roots, so there is no associated difficulty in estimating the amount of underground parts. A disadvantage, however, is that there is nc clear division between live plant, dead plant, and peat, so the terms "standing crop" and "biomass" have no useful meaning (Clymo 1970). At least part of the moss tissue remains alive at considerable depths in the peat, so biomass can by no means be equated with the green layer of the turf (Longton 1972c).

Estimates of net dry matter increase of either the Tomenthypnum nitens or the Feather moss canopies were not possible because nc measurements of decomposition rates were made. Estimates of the net production of the Tomenthypnum nitens canopy are difficult because of the considerable spatial variation in growth rates due to differences in water status, as well as the problem of relating length increment to increase in biomass. The latter point presents a complex problem because T. nitens stems of different colours (and different water contents) have different morphologies. Green stems have a very elongated growth form and a high shoot density, brown stems are less densely clustered and have a more open appearance, and yellow stems are intermediate. The density of stems varies from 4 x 10^4 to 1.5 x 10^5 per m^2, the higher shoot densities being found in moss carpets possessing green apices.

Measurements of 13 samples, each 55 cm^2, of the top 1 cm of the *T. nitens* canopy showed a mean biomass of 167 ± 13 g m^{-2} (mean±s.e.). If it is assumed that green moss represents 10%, yellow-green 30%, yellow-brown 50%, and brown 10% of the *T. nitens* carpet (from field observations); and that the green moss grew 1.6 cm, yellow-green 1.0 cm, yellow-brown 0.5 cm, and brown 0.4 cm in the 1975 season (Fig. 16); then it follows, disregarding differences in morphology, that the average net production of the moss carpet is 0.75 cm, or 125 g m^{-2}. Examination of canopy samples, however, indicated that the apices of about one-third of the individuals (including indeterminate branches) terminated below the 1 cm mark sampled above. The production estimate, therefore, should be increased by 50%, which makes the estimate of net production of the *Tomenthypnum nitens* canopy, in 1975, about 190 g m^{-2} of canopy surface. The errors in estimating this value are numerous and mostly of unknown magnitude, so no confidence limits can be set.

The value cannot be compared with other measurements since no published production values for *T. nitens* are known. It is, however, of the same order of magnitude as most published production estimates for species of *Sphagnum*; for example 200 to 800 g m^{-2} for *S. fuscum* in northern Europe (Overbeck and Happach 1956, cited in Reader and Stewart 1971), 269 g m^{-2} for *S. fuscum* in England (Bellamy and Rieley 1967), 180 to 790 g m^{-2} for various *Sphagnum* species in various habitats in the U.K. (Clymo 1970), 63 to 632 g m^{-2} for various *Sphagnum* species in Swedish tundra (Sonesson 1973), 130 g m^{-2} for *S. rubellum* in the U.K. (Clymo and Reddaway 1974), and 228 to 393 g m^{-2} for pure carpets of *Sphagnum* in the U.K. (Forrest and Smith 1975). It is also comparable to estimates of 51-145 g m^{-2} for production of *Aulacomnium palustre* in Poland reported by Teczynska-Kamecka (1974).

Estimates of net production of the Feather moss carpet are more straightfoward due to the recognizable annual growth increments. Production of *Hylocomium splendens* in 1975 could be readily estimated (see Fig. 17). Production of *Pleurozium schreberi* and *Ptilium crista-castrensis* was estimated by harvesting the current season's growth and estimating the proportion of the final growth that the sample represented. Frequently the current year's growth could not be distinguished. In such cases, for samples collected late in the season, about half of the green portion was taken to represent one year's growth (after Tamm 1953, p.39). For samples taken earlier in the season this fraction was proportionately reduced.

APPENDIX II

Maintenance of Mosses in Controlled Environment Chambers

A feature common to many, if not most, controlled environment chambers is the frequent exchange of air which is necessary to maintain isothermal conditions. Since mosses inevitably lose water if the relative humidity is less than 100%, this perpetual current of air can rapidly desiccate mosses, even at low temperatures, if they are not continually supplied with water.

Many mosses, however, may not survive if kept continuously wet. Some mosses, for example _Tomenthypnum nitens_, can be maintained under high evaporation conditions if the base of the canopy is always saturated; however other species, such as the Feather mosses, are adversely affected by water transported up through the canopy from below. Feather mosses were maintained successfully when evaporation was reduced (but not prevented) by the placement of a clear plastic sheet on the canopy surface. They appeared to be subject to fungal attack if kept continuously wet, but appeared to thrive as long as desiccation after watering was not too rapid.

Moss species appear to differ considerably in their tolerance to various combinations of these conditions but, if attention is paid to their water relations in the field, then their maintenance under controlled conditions should prove fairly straightfoward.